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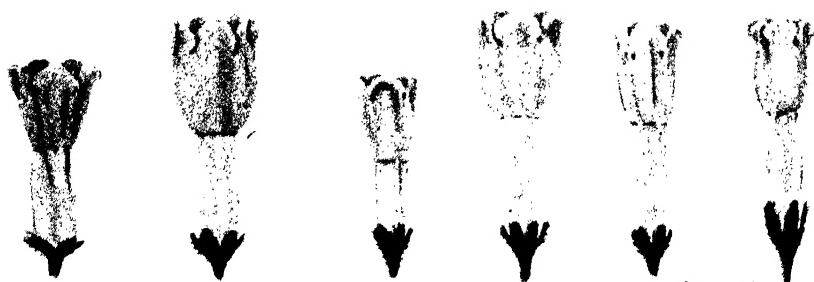
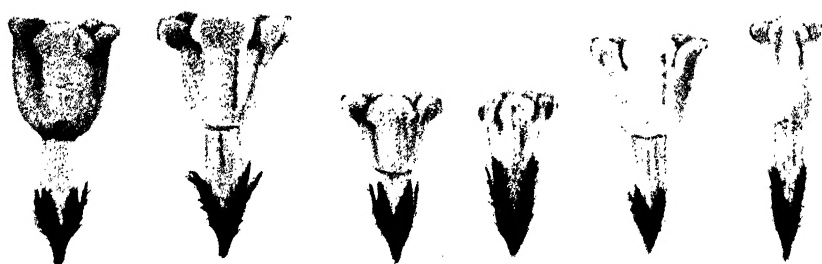
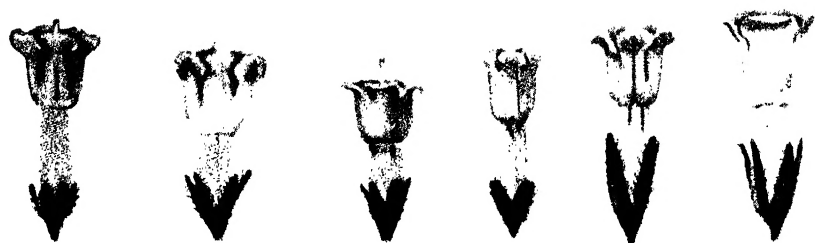
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## MERTENSIA PHYLAD

### Variation within the Species (x2)

1. *M. alpina*: alpine tundra
2. *M. lanceolata*: subalpine meadows
3. *M. pratensis*: subalpine forests
4. *M. sibirica*: brook-banks, 6,000-12,000 feet





# ADAPTATION *and* ORIGIN IN THE PLANT WORLD

THE ROLE OF ENVIRONMENT IN EVOLUTION

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PHOTOGRAPHS AND DRAWINGS

BY

EDITH S. CLEMENTS

1950

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## PREFACE

As originally planned, ADAPTATION AND ORIGIN IN THE PLANT WORLD was to have been published in a series of four booklets. The first of these appeared in 1939 and deals with adaptation in the Coastal Dune Gardens of the Santa Barbara installation, with especial reference to the factors of that habitat and the results in function and form of the plant material there. The second booklet is an account of adaptation under control in some fifteen garden habitats at Santa Barbara, including the Dune Gardens and was finished in manuscript form by 1941. The third volume of the series was to have dealt with the response to climatic and edaphic conditions in the score or more of natural gardens of the transplant transect on Pikes Peak. The fourth and final book was organized as a detailed analysis and discussion of the convergence and conversion of species at both centers, and of the ecological basis of evolution and hence of classification and the natural system.

Publication of volume II was delayed by the retirement of Dr. Clements from active association with the Carnegie Institution of Washington, and the consequent disbanding of his departmental staff. This necessitated a revision of the original plan, and resulted in combining the second and third booklets into one volume. The manuscript for this publication was practically completed by 1945 when both Dr. Clements and Dr. Long died within a few months of each other. In the following period, the experimental gardens and laboratories of the installations at Santa Barbara and Pikes Peak were dismantled and the property turned over to other purposes.

The final outcome of these successive events as they affected the original project, is represented by this publication. It comprises the material prepared for booklets II and III, with the exception of the section on histology, and includes in condensed form some of the matter reserved for book IV. It is hoped that this presentation of methods and results may serve as a guide and stimulus to other workers in the field since the subject is so vast and complex and of such fundamental importance, that it demands many years of research and many points of view for the attack on the problem and its solution.

For the information of any who may wish to consult the complete records of the researches in the experimental and transplant gardens, it should be said that these have been assembled and preserved for such purposes. The herbarium of voucher plants is located in Colorado College at Colorado Springs, and the collection of grasses in State College, New Mexico. Garden records, of all sorts and the large number of photographs can be found in the care of Mr. B. W. Allred, Soil Conservation Service, Fort Worth, Texas.

It should, perhaps, be added that no attempt has been made in this publication, to take note of any changes in nomenclature that may have occurred since the manuscript was finished in 1945.

EDITH S. CLEMENTS

La Jolla, California,  
December 15, 1949

## CONTENTS AND ILLUSTRATIONS

<i>Mertensia</i> Phylad . . . . .	Frontispiece
Preface . . . . .	iii

### I. COASTAL LABORATORY AND EXPERIMENTAL GARDENS

#### CHAPTER I INSTALLATION

Introduction . . . . .	1
General . . . . .	5
<b>Plate 1: Main Gardens.</b> . . . .	6
Nutrient Series . . . . .	7
Soil Pits . . . . .	8
<b>Plate 2: Soil Pits in Main Garden</b> . . . . .	9
Dune Soils . . . . .	10
<b>Plate 3: Coastal Dune Gardens</b> . . . . .	11
Lath-house Series . . . . .	10
<b>Plate 4: Lath-houses</b> . . . . .	12
In-and-out Huts . . . . .	10
<b>Plate 5: In-and-out Huts</b> . . . . .	14
Water-light Series . . . . .	13
Oak-shade Series . . . . .	13
<b>Plate 4: Oak-shade Transect</b> . . . . .	12
Length-of-day Tents . . . . .	16
<b>Plate 6: Length-of-day Tents.</b> . . . .	15
Competition Cultures . . . . .	18
<b>Plate 7: Competition Plots</b> . . . . .	17
Acclimatization . . . . .	18
<b>Plate 8: Transplants from Pikes Peak         to the California Coast.</b> . . . .	19
Materials . . . . .	20

#### CHAPTER II

#### FACTOR, FUNCTION AND FORM

FACTOR . . . . .	22
Main Garden . . . . .	22
Nutrients . . . . .	23

## vi ADAPTATION AND ORIGIN IN THE PLANT WORLD

Soils . . . . .	23
Length-of-day Tents . . . . .	23
Lath-house . . . . .	24
In-and-out Huts . . . . .	25
Dune Gardens . . . . .	26
FUNCTION . . . . .	27
Transpiration . . . . .	27
Sealed Phytometers . . . . .	27
Ecad Series Short-period Values . . . . .	30
FORM . . . . .	35
Phytometers . . . . .	35
<i>Helianthus</i> Series I . . . . .	35
<i>Helianthus</i> Series II . . . . .	37
Plate 9: Sealed and Free Phytometers . . . . .	39
Correlations . . . . .	40
Soils and Nutrients . . . . .	40
Plates 10-20: Changes in form due to soil factors . . . . .	45-54
Lath-houses . . . . .	41
Oak-Transect . . . . .	41
Plates 21-22: Changes in plant form due to shade . . . . .	55-56
Length-of-day Series . . . . .	41
Plates 23-29: Changes in form due to time exposure to sunlight . . . . .	57-59
Competition Cultures . . . . .	42
Plates 26-29: Effects of competition on plant form. . . . .	60-63
Plates 30-34: Adaptations to a complex of factors as recorded in Tables 12 and 13 . . . . .	64-68

## CHAPTER III

### BEHAVIOR

Kinds of Rhythm . . . . .	69
Materials and Technique . . . . .	70
Adaptation in Flowering Period . . . . .	71
Change from Summer to Winter Blooming . . . . .	72
Change from Summer to Spring Blooming . . . . .	75
Plates 35-37: Changes in Blooming and Life-form . . . . .	76-78
Flowers Opening One-Two Months Early . . . . .	79
Stable Summer Bloomers Mostly a Month or Less Earlier . . . . .	81
Repeats and Ever-Bloomers . . . . .	82

## CONTENTS AND ILLUSTRATIONS

vii

Rhythm in Factor Gradients . . . . .	86
Dates of Blooming in the Nutrient-Water Series . . . . .	87
Dates of Blooming in the Lath-House Series . . . . .	88
Dates of Blooming in the Soil-Pits Series . . . . .	88
Dates of Blooming in the Length-of-Day Series . . . . .	89
Behavior in Acclimatization . . . . .	90
Nature and Scope . . . . .	90
Survival Value . . . . .	91
Climaxes and Experimental Materials . . . . .	92
Acclimatization Experiments at Santa Barbara . . . . .	93
Species from Warm Climates . . . . .	94
Acclimatization Experiments in Coastal Dunes . . . . .	96
Role of Volunteers . . . . .	98
Establishment of Volunteers . . . . .	98
Graphs . . . . .	100
Tables . . . . .	110

## II. ALPINE LABORATORY AND TRANSPLANT GARDENS

### CHAPTER IV

#### INSTALLATION

Introduction . . . . .	131
<b>Plate 38: Engelmann Canyon: Location of the</b>	
<b>Laboratory Buildings and Montane Station . . . . .</b>	<b>130</b>
Transplant Gardens . . . . .	132
General . . . . .	132
Plains Station . . . . .	132
<b>Plate 39: Plains Station at 6,000 feet . . . . .</b>	<b>133</b>
Montane Station . . . . .	135
<b>Plate 40: Sun-moist and Sun-wet Gardens . . . . .</b>	<b>134</b>
<b>Plate 41: Sun-dry and Dry-shade Gardens . . . . .</b>	<b>136</b>
Alpine Station . . . . .	135
<b>Plate 42: Gardens and Buildings at 12,000 feet . . . . .</b>	<b>138</b>
<b>Plate 43: Transplant Plots and Gopher-garden . . . . .</b>	<b>139</b>
<b>Plate 44: Slag-pile and Ravine Plots . . . . .</b>	<b>140</b>
Midalpine Stations . . . . .	141
Seasonal Phytometers . . . . .	141
Free Phytometers . . . . .	141
Sealed Phytometers . . . . .	142



Short-Period Phytometers . . . . .	143
Standard . . . . .	143
Native . . . . .	144

## CHAPTER V

## FACTORS AND CONTROL

Methods and Results . . . . .	146
<b>Plate 45: Instrumentation at the Montane Station</b> . . . . .	147
Plains Station . . . . .	148
Sun-Garden . . . . .	148
Lath House . . . . .	148
Montane Station . . . . .	149
Moist-sun Garden . . . . .	149
Dry-sun Garden . . . . .	149
Lath Houses . . . . .	149
Dry-shade Garden . . . . .	150
Wet-shade Garden . . . . .	150
Wet-sun Garden . . . . .	150
Alpine Station . . . . .	150
Climax . . . . .	150
Subclimax . . . . .	151
Gopher Mound . . . . .	152
Slag Pile . . . . .	152
Lath Houses . . . . .	152
Ravine . . . . .	152

## CHAPTER VI

## FUNCTIONS

Transpiration . . . . .	154
Seasonal Phytometers . . . . .	154
Short-period Phytometers . . . . .	154
Climatic Series . . . . .	154
Edaphic Series . . . . .	155
Native Phytometers . . . . .	156
Detached Shoots and Leaves . . . . .	159
Osmotics . . . . .	160

# CONTENTS AND ILLUSTRATIONS

ix

Growth . . . . .	161
Seasonal Free Phytometers . . . . .	161
Plains Station . . . . .	161
Montane Station . . . . .	161
Alpine Station . . . . .	162
Comparison of Stations . . . . .	162
Mean Growth Rates . . . . .	163

## CHAPTER VII

### ECOGENESIS

Nature of Species . . . . .	166
The Genetic Definition . . . . .	166
The Evolutionary Definition . . . . .	167
Experiment . . . . .	168
In Nature . . . . .	168
Under Control . . . . .	168
Methods . . . . .	169
Nature's Experiments . . . . .	171
Montane Ecads . . . . .	172
<b>Plates 46-52: Natural Ecads at 8,000 feet . . . . .</b>	<b>174-180</b>
Alpine Ecads . . . . .	173
<b>Plates 53-55: Natural Ecads at 12,000 feet . . . . .</b>	<b>181-183</b>

## CHAPTER VIII

### CONTROLLED EXPERIMENTS

Gardens . . . . .	184
Methods and Objectives . . . . .	184
Transplants . . . . .	185
Factors . . . . .	185
Exsiccati and Photographs . . . . .	185
Records . . . . .	187
Sun and Shade Transplants . . . . .	187
Reciprocals . . . . .	187
<b>Plate 56: Conversions of <i>Mertensia lanceolata</i> and <i>pratensis</i> . . . . .</b>	<b>186</b>
<b>Plate 57: Adaptations of <i>Mertensia sibirica</i>. . . . .</b>	<b>188</b>
<b>Plates 58-59: Conversion of <i>Erigeron glabellus</i></b>	
<b>and <i>macranthus</i> . . . . .</b>	<b>190-192</b>
<b>Plate 60: Sun and Shade Reciprocals of <i>Smilacina stellata</i> . . . . .</b>	<b>194</b>

<b>Plate 61: Sun and Shade Transplants of <i>Rosa sayi</i></b>	
<b>and <i>engelmanni</i>, and <i>Senecio fendleri</i></b>	195
<b>Plate 62: Sun and Shade Ecads at 8,000 feet</b>	197
Altitude Transplants	196
Factors in Alpine Dwarfing	196
Water	196
Light	198
Temperature	198
Length of Season	198
Humidity and Transpiration	198
Transplants from Higher to Lower Altitudes	199
<b>Plates 63-65: Transplants from 12,000 feet</b>	
<b>to Montane Shade at 8,000</b>	200-204
<b>Plates 66-67: Transplants of <i>Campanula rotundifolia alpina</i></b>	
<b>from Higher to Lower Altitudes</b>	205-206
<b>Plate 68: Adaptations of <i>Achillea millefolium</i></b>	207
<b>Plate 69: Ecads of <i>Carduus ericephalus</i></b>	208
<b>Plate 70: Dwarf Ecads of <i>Rudbeckia hirta</i></b>	210
Transplants from Lower to Higher Altitudes	202
<b>Plate 71: Montane species transplanted from 8,000 to 12,000 feet</b>	212
Fixation	209
Hybridization	213
In Nature	213
Under Control	214
Methods and Results	215
Stomata as Indexes of Adaptation	216
Methods	216
Applications and Results	217

## CHAPTER IX

### EXPERIMENTAL MORPHOGENY

Definition	218
Methods and Materials	219
Competition and Correlation in the Plant Body	219
<b>Plate 72: Terads of <i>Digitalis gloxinoides</i></b>	221
<b>Plate 73: Terads of <i>Baptisia leucophaea</i></b>	
<b>and <i>Psoralea tenuiflora</i></b>	222
Natural Mutants	223

Manipulation of the Plant . . . . .	224
Mutilation . . . . .	224
Injection . . . . .	225
<b>Plate 74: Terads Induced by Manipulation . . . . .</b>	227
Manipulation of the Habitat . . . . .	226
Hypertrophy . . . . .	226
<b>Plate 75: Terad of <i>Helianthus annuus</i> . . . . .</b>	228
<b>Plates 76, 77: Terads of <i>Plantago lanceolata</i> . . . . .</b>	231-232
Hypotrophy . . . . .	230

## CHAPTER X

### PHYLOGENY

Phylads . . . . .	233
<i>Lupinus</i> Phylad . . . . .	233
<i>Mertensia</i> Phylad (Frontispiece) . . . . .	234
Convergence and Conversion . . . . .	234
Significance . . . . .	234
Composites . . . . .	235
<b>Plate 78: Involucres Overdeveloped in Shade . . . . .</b>	237
<b>Plate 79: <i>Artemisia scopulorum</i> to <i>pattersoni</i>;       <i>Solidago nana</i> to <i>humilis</i> . . . . .</b>	239
<b>Plate 80: <i>Senecio bigelovi</i> to <i>cernuus</i>;       <i>Helianthella quinquenervis</i> to <i>parryi</i> . . . . .</b>	240
<i>Solidago</i> Phylad . . . . .	238
<i>Senecio</i> Phylad . . . . .	238
<b>Plate 81: <i>Senecio taraxacoides</i> to <i>amplectens</i> . . . . .</b>	242
<b>Plate 82: <i>Senecio fremonti</i> in native habitat;       <i>Senecio taraxacoides</i> to <i>fendleri</i> . . . . .</b>	244
<b>Plate 83: <i>Senecio croceus</i> Ecads . . . . .</b>	245
Grasses	
Text-figures 1-7, and Tables . . . . .	262-272
<i>Festuca</i> Phylad . . . . .	246
<i>Agropyrum-Elymus</i> . . . . .	246
<b>Plate 84: Ecads of <i>Elymus canadensis</i> . . . . .</b>	248
<b>Plate 85: Ecads of <i>Agropyrum scribneri</i> and <i>Bromus purgans</i> . . . . .</b>	249
<i>Stipa</i> Phylad . . . . .	247

## CHAPTER XI

### SUMMARY AND CONCLUSIONS

Methods and Materials . . . . .	252
Genetic Tests . . . . .	253
Adaptation . . . . .	254
Correlation and Manipulation . . . . .	255
Ecads and Ecotypes . . . . .	256
Convergence and Conversion . . . . .	257
Species and Phylads . . . . .	258
Climatic cycles and mass Migration . . . . .	259
Conclusions . . . . .	260

### APPENDIX

Text-figures and Tables of Grasses . . . . .	262
Graphs . . . . .	273
Tables . . . . .	282
Glossary . . . . .	309
Supplemental References . . . . .	314
List of Species from Europe . . . . .	319
Index . . . . .	325

PART I

COASTAL LABORATORY AND  
EXPERIMENTAL GARDENS



I.  
THE COASTAL LABORATORY AND  
EXPERIMENTAL GARDENS

CHAPTER 1  
INSTALLATION

**Introduction.**—To the dynamic ecologist, adaptation is the basic process by means of which both plant and community fit themselves to their common environment. The modification of the species-individual, or specient, leads to the differentiation of the community, which then undergoes its own peculiar adaptation as a complex or super organism. Both types of organism are under the immediate control of the physical factors of the habitat, and the adjustment of either one to changed or changing conditions is necessarily reflected by the other. The causative process is initiated by climatic cycles, of which the major are diastrophic in origin, while the minor ones are solar. The respective dry-warm and moist-cold phases constitute the compulsive force that sets in motion vast migrations, during the course of which great changes are wrought in specients and climaxes.

Habitats are altered, species are shifted, modified or extinguished, and these changes are then felt by the community, which undergoes corresponding transformations. All these weave the pattern of an integrated process of evolution that is an epitome of the dynamic interaction of life and environment, and constitutes the paramount theme of ecology.

In its essence, ecology is concerned with cause-and-effect relations in nature, but it recognizes that the processes and organisms originating here pass over into all the phenomena of life. The proper understanding of these must be sought first in nature or finally carried back to it, since all natural law necessarily had its origin there. Consequently, the principles for the program in experimental adaptation have been drawn from the out-of-doors, and the results have been constantly referred to it for interpretation and correction. This has demanded a new type of experimentation, the essential feature of which had earlier been pointed out by Bacon, Naegeli, Kerner and Bonnier, but this has been expanded into a comprehensive system of natural and control gardens to include all the major approaches to the problem of adapta-



tion as one of the keys to the origin of species and communities. The signal advantage in the project has been the clisere of climates and climaxes available on Pikes Peak, which have been effectively supplemented by subtropical and marine climates at Santa Barbara.

The term adaptation is often employed loosely in a general sense, as well as in the static meaning to denote fitness as a consequence of selection. By contrast with these is the ecological usage which is based upon the assumption that adaptation is an actual process by means of which new forms of varying rank arise from existing older ones. This may come about by the modification of the habitat or by migration into other habitats. In experimentation, the simpler procedure is to sow or plant in different sites, but it is sometimes desirable to modify factors without disturbing plants already established in them.

The first objective of the present series of investigations has been to ascertain whether adaptation is a process or merely a selecting-out of strains already present. The second task is to determine how universally it operates upon flowering plants, and incidentally upon cryptogams. Following this comes the inquiry as to what factors are directly causal and what ones are indirect to the extent of acting through these. Associated with this are the questions as to whether the imprint of each factor is a distinctive one, and whether a quantitative correlation exists between the factor and its characteristic response. Directly related is the query whether a graded series can be produced between the two extremes of response. The final objective deals with the causal connection between measured factors and the criteria employed for species and their subdivisions, and this leads straightway to studies in the convergence and conversion of existing species and subspecies and the origin of new forms of different degree.

The quantitative investigations in nature and origin of habitat, species, and community were organized at Pikes Peak in 1900, and the first transplants and sowings were made there and at Lincoln, Nebraska, the following year. The instrumental analysis of the many climatic and edaphic habitats, the quadrat and transect study of the corresponding communities, both climax and successional, and the integration of some 2000 minor or "split" species with the original units or linneons occupied most of the next decade and a half. During this time, exploratory transplanting was carried on and experiments in adaptation were made under semi-control and in plant-houses. Under the auspices of the Carnegie Institution of Washington, the experi-

mental attack upon species was greatly expanded at Pikes Peak in 1918, the field of experimental taxonomy was outlined, and the three major series of transplant gardens were organized at Pikes Peak, in the Sierra Nevada Mountains and through the Great Plains. In this phase of the project, Dr. H. M. Hall and Dr. J. E. Weaver were the chief collaborators; Dr. G. W. Goldsmith, Dr. F. L. Long, Dr. E. V. Martin and Dr. C. J. Whitfield were in direct charge of the work in instrumentation, function and growth, while Dr. A. E. Douglass was engaged in cycle research, and Dr. E. S. Clements was field assistant, photographer and artist.

In the integration of the many aspects of the evolution of habitat, specient and community, a number of publications have been completed which record the results in the various contributing projects. The scope and contribution of each of these is indicated by the following titles and although time, circumstance and budget restrictions have conspired to set limits to the original plan, most of the ground has been covered and the foundations of dynamic ecology laid in respect to the major features.

- 1901 Fundamental Principles of Vegetation
- 1902 Formation and Succession Herbaria  
Herbaria Formationum Coloradensium
- 1904 Development and Structure of Vegetation
- 1905 Research Methods in Ecology
- 1906 Relation of Leaf Structure to Physical Factors
- 1907 Plant Physiology and Ecology
- 1908 An Ecologic View of the Species Conception
- 1909 Darwin's Influence upon Plant Geography and Ecology
- 1910 Life History of Lodgepole Burn Forests
- 1913 Rocky Mountain Flowers
- 1915 Herbaria Ecadium Californiae
- 1916 Plant Succession
- 1918 Scope and Significance of Paleo-ecology
- 1919 Climatic Cycles and Tree Growth I  
Ecological Relations of Roots
- 1920 Plant Indicators  
Root Development in the Grassland Formation
- 1921 Aeration and Air-Content  
Behavior of Stomata  
Drouth Periòds and Climatic Cycles

## ADAPTATION AND ORIGIN IN THE PLANT WORLD

- 1923 Experimental Pollination  
Phylogenetic Method in Taxonomy
- 1924 Experimental Vegetation  
Phytometer Method in Ecology
- 1928 Plant Succession and Indicators  
Climatic Cycles and Tree Growth II
- 1929 Experimental Methods in Adaption and Morphogeny  
Climatic Cycles and Changes of Vegetation  
Plant Ecology  
Plant Competition
- 1932 Anthokinetics
- 1934 Relict Method in Dynamic Ecology
- 1935 Further Studies of Elongation and Expansion in  
*Helianthus* Phytometers.
- 1936 Environment and Life in the Great Plains  
Nature and Structure of the Climax  
Origin of the Desert Climax and Climate  
Studies in Plant Physiology  
Plant Ecology, 2nd. ed.
- 1938 Climatic Cycles and Human Populations  
Bio-ecology
- 1939 Adaptation and Origin in the Plant World  
I. Factors and Functions in Coastal Dunes.

The present book is devoted to adaptation under more or less control of a particular factor in the gardens at Santa Barbara, and with modifications in the climatic and edaphic transplant gardens at Pikes Peak, including experimental evidence for the convergence and conversion of species, and the production of new forms of varying rank. The publication of the results of these researches in adaptation will be restricted to the actual data and their interpretation, since an adequate account of the pertinent literature in the field of evolution would require no small book in itself. The first volume of "Adaptation and Origin in the Plant World" has already appeared under the title "Factors and Functions in Coastal Dunes" (1939). It is devoted to the phytometric measurement of this unique seral habitat, which is much the same the world over. The functional and structural responses are considered in the light of xerophytism and this has led to a more exact refinement of the concept itself. The typical dwarf and prostrate

life-forms are referred to this, and the general similarity to alpine dwarfs is indicated.

Though the theme will recur from time to time, it seems appropriate to emphasize at the outset the major conclusion from an experience of forty years in ecological analysis and synthesis. The basic axiom of dynamic ecology is fully confirmed as the cause-and-effect sequence in nature, which is necessarily to be regarded as the touchstone to all natural phenomena. The utilization of this at all times and in all places becomes the primary duty of the dynamic ecologist, to whom the three watchwords, measurement, experiment, and development serve as the open sesame to all fundamental research in life sciences.

However, it must be frankly stated that this vast area contains many pitfalls and demands ever greater perspective and insight. Even after many years of investigation, it bristles with difficulties and abounds in disappointments. The continuous improvement of tools, both instruments and methods, is the overruling task, and always with the realization that it can never be completely finished, since the most exacting laboratory control in field and garden will remain a will-o-the-wisp. Hence nature, garden and laboratory must be combined in reciprocal fashion, but even this produces a twilight zone of interpretation between, that has so far proved inescapable. Accordingly, too much emphasis can hardly be placed upon the fact that the adaptation and evolution of species and community constitute research for a life-time rather than an occasional excursion into a fascinating field.

**General.**—The adaptation series at Santa Barbara were organized to complement the transplant gardens at the Alpine Laboratory, for the most part through the partial control of particular factors or factor complexes. In the case of soil-pits, dune-sands, nutrient-pans, lath-houses, in-and-out huts, and competition, the control was essentially automatic, while in nutrient-water series, length-of-day tents and sheds, and dry-soil beds, frequent or daily attention was required to maintain conditions. In addition, the main or "neutral" garden was utilized as a general control for testing candidates for experimental use, for selfing, crossing, and for such manipulations as injection, mutilation, etc. With the exception of the factor concerned, all installations were exposed to the direct action of the weather throughout the period from December to June. However, in the nutrient and the dry unit of the nutrient-water series, it was necessary to cover the pans and beds be-

PLATE 1



Main Garden at Santa Barbara.  
A. Test plots for crossing and selfing.  
B. Plots for morphogenic manipulation:  
(*Digitalis gloxinoides*: Plate 72).

fore each rain, a requirement that resulted in the elimination of these groups after a few seasons, owing to the tendency of rains in California to begin during the night (Plate 1).

The soil of the main garden is a natural unfertilized loam with a moderate sand fraction, but sufficient colloidal matter to "run together" and form a crust, a feature that demanded frequent cultivation to permit thrifty growth. The dune soils were fairly typical of such areas and were much alike in both ridge and shelter habitats with respect to chemical properties. The "blow-sand" of the ridge was exceedingly permeable and dried out with corresponding rapidity; in the shelter garden the sand was more compact, but its peculiar qualities were a surface layer so impervious that water would stand on it for several hours, together with a water-table within the reach of deep-rooted species. Though some studies were made on the strand and fore-dunes with a saline element, it was early found impossible to grow experimental species on such sites.

While the complete installation for semi-control comprised 12 different types, the number of direct factors utilized was but three, namely, water, nutrients, and light. Temperature was brought into the study of rhythm and into manipulation experiments, but only in a preliminary manner. However, both this factor and wind, as well as humidity, were separately employed in quantitative tests of transpiration in a sealed dark-room with conditions otherwise uniform (Martin 1936). To soil-water or holard are to be referred the soil-pits, swamp-tanks and dune-sands in particular; the nutrient-water series and nutrient pans were primarily concerned with fertilizers and special minerals. The competition cultures exhibited a complex of factors, in which water was most important, nutrients usually second and radiation third (Clements, Weaver and Hanson, 1929). The response to light was tested directly in lath-houses, in-and-out huts and in natural oak shade, and for terms of day-length in the tents and sheds specially designed for this purpose.

**Nutrient Series.**—Initial tests demonstrated that most species "burned out" under the California sun with increases of fertilizer and that water must be added as a compensation. In consequence, this installation was known as the nutrient-water series (NW). Three plots were regularly used for each species, one in unmodified loam serving as a check, since it received rainfall alone. A fourth plot was

similarly without fertilizer, but the holard was reduced to about half by means of a canvas cover to exclude rain. This device was satisfactory during the drier years, but in wet seasons the gradient could not be maintained, chiefly because of unexpected rains at night. To the second bed were added 500 grams of Vigoro, a commercial fertilizer composed of blood-meal, urea, bone, and added chemicals. A measured amount of water adjusted to the rainfall was also supplied to this plot, while number three was treated with 1000 grams of Vigoro and twice as much water was added as to the second bed. These graduated treatments are denoted in the text and tables as NW-, NW-0, NW-1, NW-2 respectively.

The plots were 5 feet square and each contained 16 to 24 individuals in accordance with the stature of the plants. Twenty-four species were tested each year and a total of about 200 were employed altogether, many of them represented by both selfed and open populations. Practically all of these were annuals or early flowering perennials, since the change to summer conditions rendered it desirable to terminate the experiment early in June.

**Soil-pits.**—The three permanent series consisted of six pits, 7 feet long, 3 wide and 2 deep; each series being filled with rich loam, heavy clay ("adobe"), and river-sand, respectively. The pits accommodated 6 or 12 species per season, with 24 or 12 individuals of each, depending primarily upon their vigor and size. The plants were placed 8 inches from the edge to discourage the roots from growing out into the surrounding loam and this precaution was reinforced by not watering the interval between beds and rows (Plate 2 A).

In order to distinguish the effects of soil and air factors as between the main garden and the two dune gardens, a set of three soil-pits was established in these, each set containing a pit of the soils concerned. The results from them have already been discussed in the dune volume (1939), but the pits have been maintained for further detailed studies in adaptation (Plate 2 B).

Similar in design but with a metal lining and cover were the soil pans devoted to a number of minerals with a known or supposed effect upon growth and form, such as calcium sulphate, magnesium silicate, sodium chloride, sodium carbonate, etc. After obtaining some initial results, these pans were scrapped because of the corrosion of the metal walls and consequent leakage and dilution. However, the tests with

PLATE 2



Soil Pits in Main Garden.

- A. Three series of six pits each; left to right: adobe, sand, loam.
- B. Set of three pits for comparison of soils in the three gardens; left to right:  
1. Main Garden loam; 2. Shelter Garden sand; 3. Ridge Garden sand.



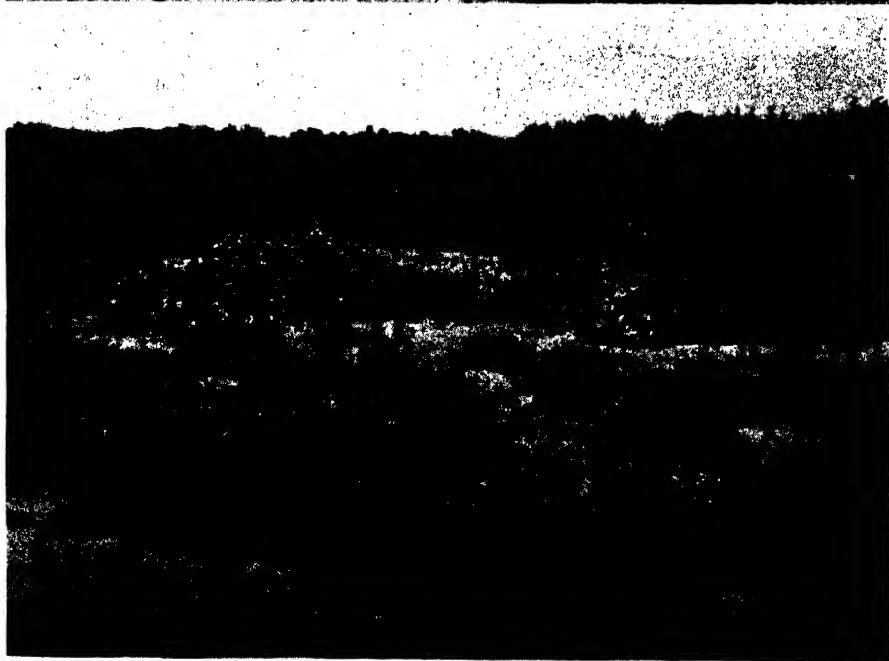
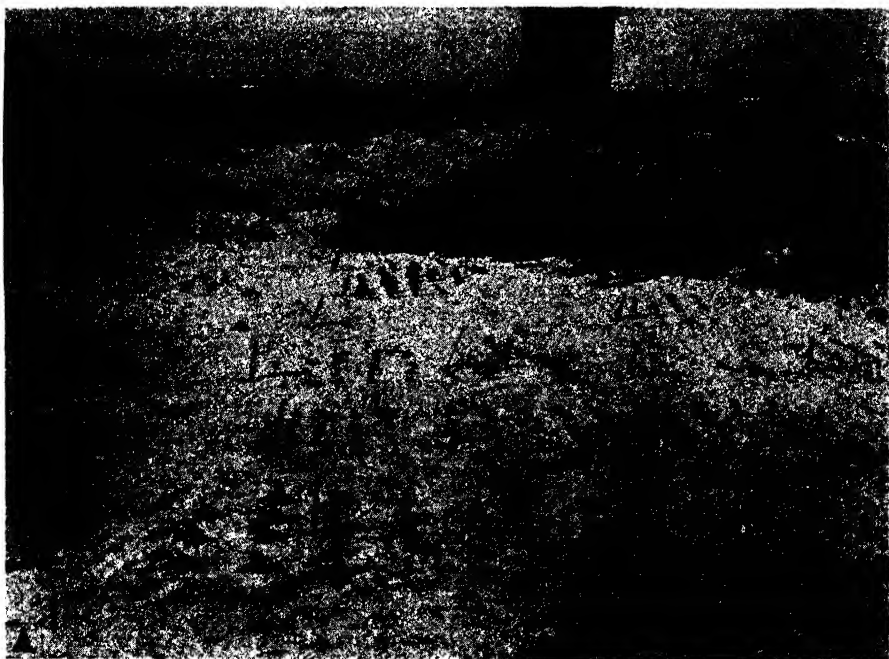
gypsum have been renewed and have yielded consistent effects in dwarfing all of the species subjected to the action of this mineral.

An original set of tanks for hydrophytes, each 10 x 12 feet in outline, was constructed to provide muck, amphibious, floating and submerged conditions. These served very well for the corresponding life-forms of hydrophytes, but added little beyond experimental confirmation of the comprehensive studies of Gluck and others. Consequently, they were filled up to form a single habitat with a loam soil maintained slightly below saturation in so far as possible, but exceeding this during protracted rains.

**Dune Soils.**—First and last a half-dozen gardens were established in a small complex of coastal sand-dunes, with the active center lying about 500 yards from the shore. The strand and brackish swamp proved too unstable for experimental purposes, and the final series consisted of ridge, knoll, and shelter gardens. The first was located on an exposed ridge of moving sand, the second on a stabilized knoll rising about five feet above the level of the shelter garden, and adjacent to it, both being protected sufficiently to prevent blowing of the sand. This was brought about in part by the rim of the encircling dunes, as well as by a wind-break of trees and a dense community of shrubby lupines. The relation to the water-table and the diversity in the respective sands have already been mentioned; a more detailed description may be found in *Factors and Functions in Coastal Dunes* (1939) (Plate 3).

**Lath-house Series.**—A large house was constructed of standard plaster lath 1  $\frac{3}{4}$  inches in cross-section and 6 feet long; this was divided into five compartments approximately 20 feet square and 6 feet high. The lath were spaced differently for each section, namely, as nearly as possible to  $\frac{43}{4}$ ,  $1\frac{3}{4}$ ,  $\frac{3}{4}$ ,  $\frac{3}{8}$  and  $\frac{3}{16}$  inches, to yield a gradient from outside sunlight to an intensity too low to permit the survival of the great majority of species. In the partitions the spacing was made wider than on the walls of the respective sections, in order to correct in some degree for the reduced amount of radiation falling upon the partition. A path 3 feet wide ran through the center of the houses, and the experimental plants were placed on either side in one or two rows depending upon the size, so that mutual shading was reduced in large measure (Plate 4 A).

PLATE 3



Coastal Dune Gardens.

A. Ridge Garden.

B. Shelter Garden with Knoll Garden beyond.

PLATE 4



Installation for Shade Experiments.  
A. Lath-house showing 75% and 50% units.  
B. Sun-shade transect beneath oak-tree.

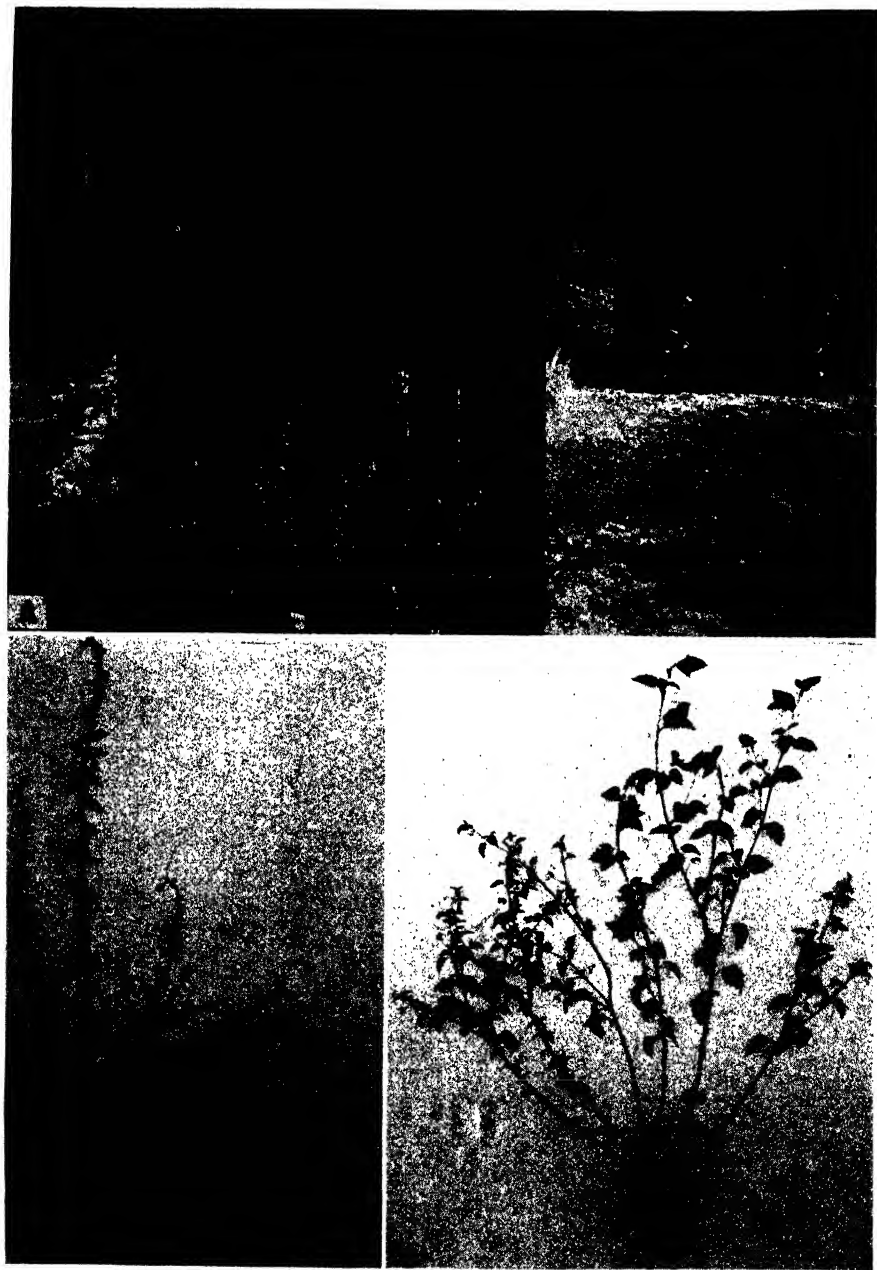
**In-and-out Huts.**—These were essentially small lath-houses about 4 feet square and 6 feet high, covered with lath placed  $\frac{1}{2}$  inch apart. Species of branching habit were selected for this study and half-grown individuals were planted close to the wall, and alternately inside and outside. After the branches had become sufficiently developed, some of those on "in" plants were carried through the spaces to the outside, with the reverse disposition for those of "out" plants. This not only produced sun and shade shoots on the same plants, but also reversed the behavior of the two kinds, sun plants and shade plants (Plate 5).

**Water-light Series.**—For these, separate lath-houses were built of wooden frames 8 x 12 feet in cross section and 6 feet high, which were covered with lath spaced like those in the five compartments of the large lath-house. In each of these were installed batteries of phytometers of the usual type in metal containers 8.5 inches in diameter and 11 inches tall. Each set comprised 6 or 8 plants and was given a different amount of water, so that the battery in each house was made up of four sets with respective holards of 14, 18, 26 and 35 per cent of the dry weight of the soil. These limits were maintained with slight variation and occasional tests were made to insure that the water was well distributed throughout the container. A detailed description of the methods employed is given by Clements and Long (1935).

**Oak-shade Series.**—A series of semi-natural habitats or eces with different light values but similar soil and water relations was constituted by a grove of native live-oaks, together with two isolated trees with different canopy densities. By this means the results secured in the several structures were more closely correlated with those in nature. The separate trees also afforded opportunity for a unique sun-shade transect in which a score of species were grown in single rows on the north side of the oak. As a consequence, an approximate third of the individuals of each species were exposed to continuous shade, the second section to half-day shade in the middle of the day, and the outer third to full-day sun. The special advantage of this arrangement was that the plants made a living graph of response with a gradual transition from one major effect to the next (Plate 4 B).

Further use of these natural shade eces was made in a series of four habitats, consisting of moist shade, dry, moist and wet sun, to imitate as closely as might be an ecial grouping often found in nature. These also permitted an illuminating comparison with the results

PLATE 5



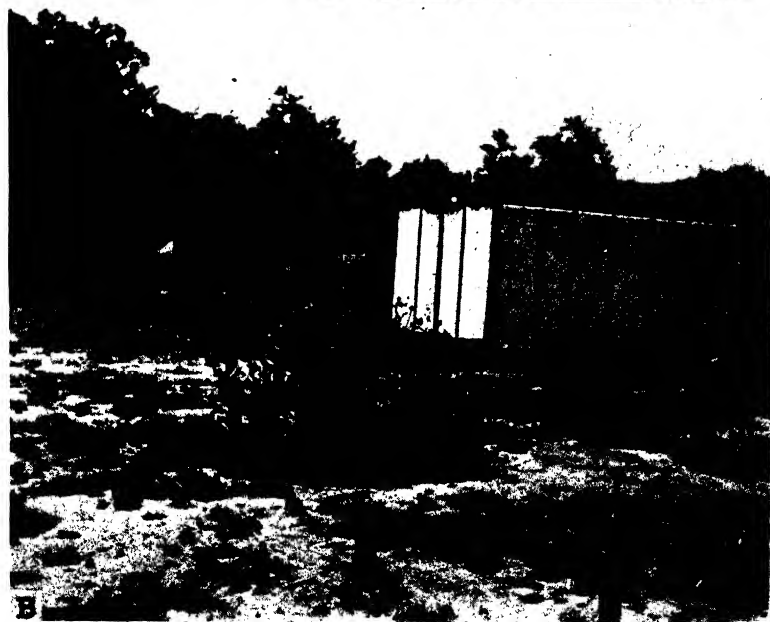
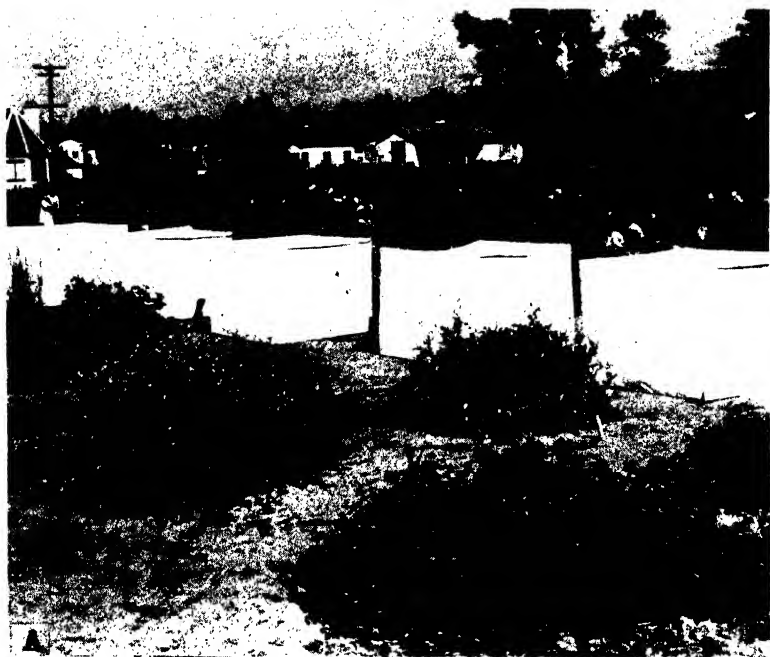
Experiments with Light and Shade.

A. In-and-out Huts.

B. *Clarkia elegans*: in-and-out.

C. *Solanum douglasii*: out-and-in.

PLATE 6



Installation for Experiments with Light and Shade.  
A. Length-of-day tents.  
B. Length-of-day shed, moving on track.

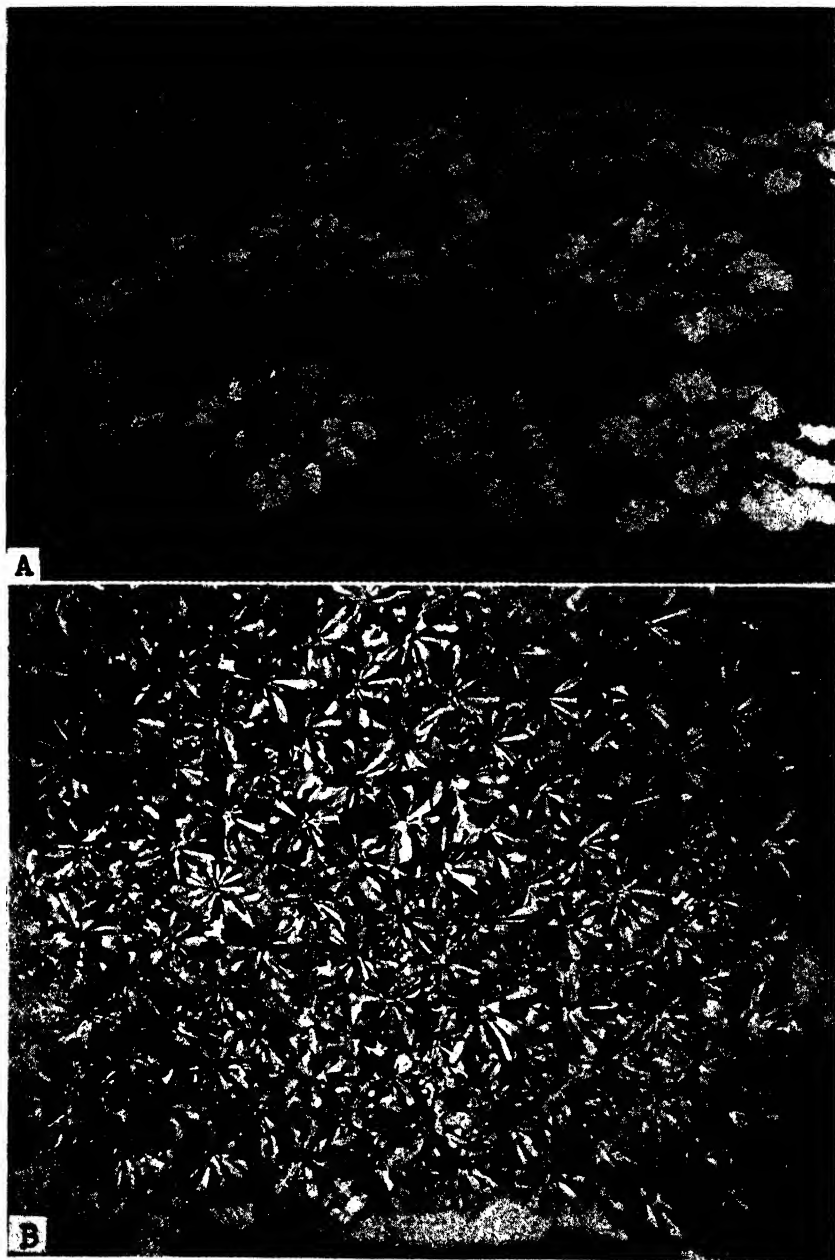
drawn from the sun-shade transect. Finally, the oaks were utilized for acclimatization studies of woodland species from the deciduous forest particularly, and they also served as partial compensation for the rainless summer of California in the case of other species accustomed to summer rains.

**Length-of-day Tents.**—In order to throw light upon growth and blooming out-of-doors during the calendar winter, two types of installation were employed to yield different day-lengths, namely, tents and sheds. The first consisted of light wooden frames, 42 x 44 x 48 inches, covered with a layer of black oilcloth to produce complete darkness and an outer one of white oilcloth to eliminate excessive heating by the sun. Tests as to light, and measurements of temperature and humidity were taken from time to time to insure that these factors were under the desired control.

Six species were employed each season and 9 or 12 individuals were planted in each plot, approximately 40 inches square. Owing to the increased evaporation and transpiration in the longer exposures, differential watering was employed to compensate, and with good practical success during most seasons. The series was based upon three different day-lengths, secured by removing and replacing the two rows of tents at the proper times. Long-day exposure was for the full day of the spring months concerned, normally 12 to 14 hours. The medium-day was 8½ (7:30 a.m. to 4:00 p.m.), and short-day 5 hours (9:30 a.m. to 2:30 p.m.). The possible effect of higher temperatures at night under the tents was checked experimentally by growing plants for one season under long-day with a tent in place at night, but no material difference could be detected (Plate 6 A).

For a supplementary installation, use was made of a wooden frame 12 feet long, 8 wide and 6 high, covered with lath to which was applied asphalt felt, followed by white oil-cloth. Each shed was built on small wheels and thus was readily moved back and forth over the metal track, an operation facilitated by double doors at one end. The day-lengths varied in different experiments but were for the most part the same as those for the length-of-day tents. The sheds were devoted largely to tests with standard and free phytometers, but also permitted the inclusion of some experimental species, to yield comparisons and correlations as to factor and function (Plate 6 B).

PLATE 7



Competition Plots.

A. Portion of 16-unit plot: *Phacelia campanularia*.

B. 256-unit plot: *Crepis alpina*.

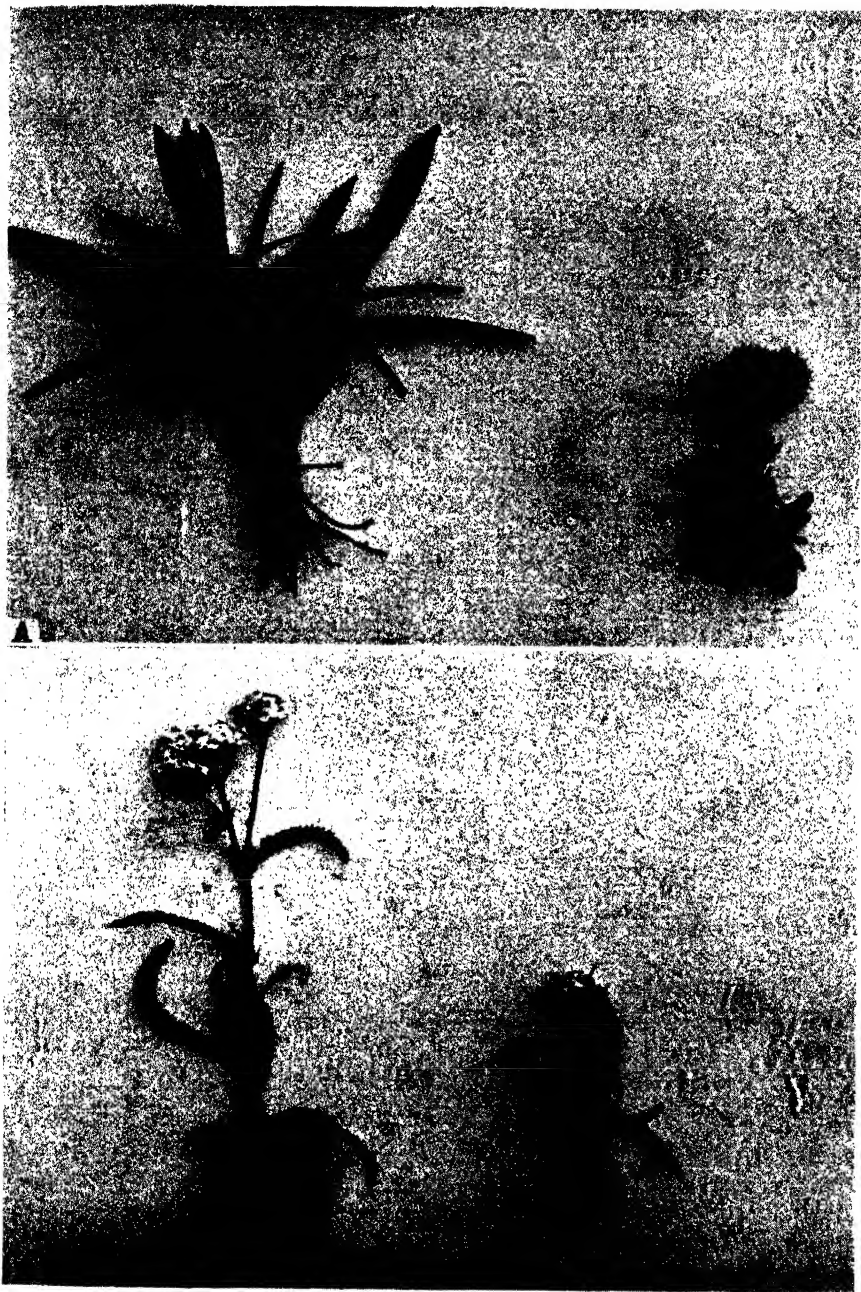


**Competition Cultures.**—For the analysis of adaptation to competitors, the primary control is secured by spacing, with the consequence that the amount of water, nutrients and light available to each individual is a function of the number of plants in a square, usually 3 or 5 feet for each dimension. The standard series consists of four plots with 4, 16, 64, and 256 plants, but the number may begin with one and run to 64 with large plants, while as many as 512 have been employed. The cultures are frequently supplemented by native and by volunteer weed and garden stands, with which densities are determined when seedlings are established and again when flowers or fruits have developed. In some species, the 4-plant bed yields optimum development and becomes a standard for the several degrees of reduction in growth, but as a rule isolated individuals alone attain the maximum for comparison. For practically all species, the densities employed produce wide differences between the plant groups, though these disappear when corner, border, dominant and suppressed plants of each are assembled to form a continuous series (Plates 7, 27, 29).

**Acclimatization.**—This process is to be regarded as that type of adaptation in which climatic factors take either a large or decisive part, and soil conditions a relatively subordinate one. It is readily perceived that nature offers an almost unlimited number of combinations of the two, and it is equally evident that the respective roles can be determined only by experimental analysis. The recognition of this fact led to the proposal of the term *ecesis* for all kinds of establishment, leaving acclimatization to denote those cases in which climate exerted the ruling effect. Further distinctions can be drawn on the basis of type and amount of compensation required and upon the degree of completeness in response.

At Santa Barbara, direct studies have been made upon some two hundred species; these were chiefly perennial herbs, with the grasses leading, but shrubs and trees were also included to the number of several score. These were drawn from a wide range of climates and climaxes, deciduous forest and prairie first, the clisere of climaxes on Pikes Peak next, and the climates of northern and central Europe last. The four major sites were oak shade for woodland species, sunny borders of the main garden for prairie ones, and the ridge and shelter gardens of the dunes for a varied group but with subtropical species well represented (Plate 8).

PLATE 8



Alpine species Transplanted from Pikes Peak to the Santa Barbara Gardens.  
A. *Gentiana frigida* and *Solidago humilus nana*.  
B. *Achillea millefolium alpina*: extreme forms.

## MATERIALS

In conformity with the synthetic nature of ecology, the endeavor has been made to employ as comprehensive a range of plant materials as possible. The actual species have been selected with reference to climax and flora on one hand and taxonomic relationship, family and genus on the other. A variety of life-forms have been taken into the plan and special attention has been directed to criteria of different rank and meaning. Much thought has been devoted to securing uniformity in populations, though it has also been recognized that heterogeneity has something to add to the analysis of adaptation.

In the complete program, several hundred species have been utilized. Cultivated species have formed a large majority in the gardens at Santa Barbara, while native ones have been regularly used in the transplant gardens on Pikes Peak. There has likewise been an intermediate group, notably of California annuals, with some background of cultivation to the extent of several decades. These have the advantage of readier germination and greater uniformity than with most species brought directly from the field. Much material has been drawn from European botanical gardens and may properly be regarded as cultivated in-so-far as the particular strains are concerned. The list of these will be found on pages 319 to 324.

The climaxes best represented in the series on adaptation and acclimatization are the mixed, true and California prairies and the deciduous forest, though many of the species have been derived from seral, i.e., edaphic, situations. Next in importance have been the three typical climaxes at the Alpine Laboratory, viz, montane, subalpine, and alpine, which with the mixed prairie have formed the groundwork for the transplant and conversion series. The families dealt with, number about a hundred and the genera several hundred, while the species all-told amount to approximately a thousand. Not more than half of these have been objects of extensive experimental analysis, the others being employed for special or contributing studies. To insure economy of time and convenience, the life-forms are for the most part herbaceous; relatively few shrubs have been utilized and no trees except for correlation experiments. Among herbs, attention has been given to both annuals and perennials, as well as a few biennials, and such subforms as rhizome and rooting species have received a considerable share of this. Because of their number and importance, apart from reasons to be dis-

cussed later, grasses and composites have had a major role in the various gardens. At the same time, the number of genera drawn from lower orders in the natural system of angiosperms has been kept commensurate, with the object of testing ecological responses over the six major lines of evolution among flowering plants.

With respect to the experimental individuals, a consistent endeavor has been made to have them as uniform as possible. In large degree this has been accomplished by selfing and in addition by selection before transplanting seedlings. In self-sterile forms, selection alone can be employed in the case of the annuals, though as indicated later, under the conditions of semi-control no essential difference was found in the great majority of species between populations from open and selfed seed. Annuals as a rule do not permit the use of clones, but in the case of perennials, clones and adults from both kinds of seed have been used. However, in the transplant gardens where plants are subject to natural conditions for the most part, the survival of clones is much smaller than that of adult transplants, while the latter not only grow more normally but for this reason also usually respond better to the pressure of ecial factors.

In the case of plants returned to the original habitat, they give even greater assurance as to the nature of the change. Finally the response made by adults and clones of the same species or ecad has been found to be of the same kind and degree, and hence the poorer survival of the latter led to the use of clones primarily as checks. Plants with tap-roots can be divided only with difficulty and meet with almost prohibitive mortality in the case of xerophytes. Composites in particular are unsatisfactory, with certain exceptions such as *Achillea*, while both bunch and rhizome grasses yield clones readily, as do alpine herbs of certain species. To furnish a check upon uniformity, tall and short individuals as similar as possible in each group have been utilized in transplanting, both originally and in returns (Plate 8 B).

## CHAPTER II

### FACTOR, FUNCTION, AND FORM

#### FACTOR (Tables 1-3)

**Main Garden.**—In presenting the factors of the various conditions of semi-control in the experimental garden, it will be convenient to discuss the factors of the various habitats in relation to a standard, such as the normal conditions in the main garden.

Santa Barbara is located on the coast at a latitude of  $34^{\circ} 25' N$ , with a mean annual rainfall of about 16 inches. The usual range of precipitation is from 12 to 22 inches, though the extremes are 4.49 in 1877-78 at the sunspot minimum and 45 in 1940-41 following the high sunspot plateau and drouth of 1936-39. This ratio of 1:10 is one of the most exceptional for the country. The prevailing westerlies from over the ocean exert a marked effect upon extremes of temperature by comparison with the interior valleys and help to maintain a fairly equable subtropical climate. The rainy season proper extends from late November to April. Occasional rains may occur in early autumn or in late spring, but the dry season in general approximates six months, during which the grasslands become parched and brown. Frost may occur during January and February, but freezing is rare and native vegetation almost never suffers injury. Fog is frequent during late spring and summer and affords considerable compensation to experimental materials, especially in connection with acclimatization.

The average daily maximum (by weeks) of air temperature for the season from December to May ranges from  $55$  to  $80^{\circ} F.$ , with the lowest value usually occurring in February. The average daily minimum varies between  $35$  and  $55^{\circ} F.$ , while the 24-hour average lies between  $45$  and  $65^{\circ} F.$  Records of environmental factors have been made over a period of nearly ten years, but only the two seasons of 1938 and 1939 are included in the present account. These values are shown in graphs 1 to 6.

Relative humidity is fairly high for this region, the average daily minimum varying from 20 to 80 per cent, with a seasonal average of about 50 per cent. The 24-hour average for the season is between

70 and 80 per cent. Wind movement is seldom more than a light breeze, the average rate being between 1 and 2 miles per hour.

On account of relatively low temperatures, high relative humidity, and low wind movement, rates of evaporation are not high. The maximum rate of loss from white spherical Livingston atmometers that has been observed during this time of year is less than 300 ml. per week, and during most of the season it is less than 200 ml. Evaporation from a shallow pan seldom exceeds 2 inches of water per week.

Soil temperatures at a depth of 4 inches range from 40 to 85° F. during this part of the year, with the average for the period being between 55 and 60° F.

**Nutrients.**—Since the plots for all three of the treatments in this series were close to each other and in the sun, the only factors of the environment that would be expected to show appreciable and significant differences are those of the soil. A record of holards at depths of 4 and 12 inches for most of the growing season of 1939-40 is given in table 1, from which it can readily be seen that in this respect there is no very considerable difference between the various treatments.

No measurements of soil fertility factors have been made, but the addition of Vigoro undoubtedly provides a stimulus for growth of the plants, since the size of the plants is regularly larger with the double and triple amounts employed experimentally.

**Soils.**—In this group, as with nutrients, the important factors are those in the soil. Values of holard are shown in table 1 for the season of 1939-40, the sand containing much less water than either the adobe or the loam. Field capacities, wilting coefficients, and mechanical analyses of the various soils employed in the adaptation garden are given in table 2. In addition to differences in holard in this series, it is also assumed that soil fertility is of the first importance in producing the observed differences in plant growth. The results of a chemical analysis of the various soils are given in table 3.

**Length-of-day Tents.**—Records of air temperature and relative humidity for the season of 1938-39 in the full-day, medium-day and short-day sheds appear in graph 4. The average daily maximum temperature for the entire season averages about 1° F. higher in the sheds than in the sun, while the average daily minimum is also higher than in the sun by the same amount. The resulting 24-hour average tem-

peratures are also in the same relation. Relative humidity differences are within the limits of error of the instruments, and like temperature are without material effect.

No records of air temperature under the small length-of-day tents are available, since there was not sufficient space for a shelter house for a hygrothermograph. However, some measurements made with a thermometer indicated that temperature differences between tent and outside of more than 2 or 3 degrees F. are rare. When the surface of the soil is dry, the temperature of the air within a foot of the soil surface may be a few degrees above that outside, but if it is wet, the air may be cooler than that outside.

Radiation is entirely cut off in the reduced-day habitats except for the period during which the sheds are removed, when the intensity is of course equal to that of normal sunlight at the time. The reduction in total amount of energy received on a horizontal surface is not nearly so great as the day-lengths would indicate. The total radiation impinging on a horizontal surface during a clear day in the 4-hour shed is approximately 64 per cent of the normal sunlight at the winter solstice and about 45 per cent at the summer solstice. For the 8½-hour shed, the percentage ranged from 99 to 85.

Soil-moisture values were maintained at approximately the same level for all length-of-day conditions, as shown by the data in table 1. For these habitats, no soil moisture samples were taken previous to the first of April, since rainfall, in conjunction with low evaporation and transpiration rates, maintains the soil at near the field capacity. Only after this time of year does the soil moisture deviate appreciably from this level.

**Lath-house.**—Records of air temperature and relative humidity for two of the lath-houses are shown in comparison to the sun station in graph 5. These records show that the average daily maximum air temperature in the sun averages only about 1° F. above that in lath-house 10%. The average daily minimum is a little higher in the lath-house than outside, approximately 1 to 2 degrees F., and the 24-hour average is practically the same in all sun and shade habitats.

Soil temperature is appreciably lower in the lath-houses, the decrease being progressive from the sun to the house with 5% radiation. The greatest difference is in the average daily maximum, with relatively little difference in the average daily minimum. Some records are portrayed in graph 6.

Since there usually is some wind movement in this region, the relation of relative humidity in the lath-houses to that in the sun habitat is determined principally by the respective air temperatures. In the sun, the values of relative humidity run slightly lower during the day than in the lath-houses, and higher at night, with the 24-hour averages approximately equal. Certain records are shown in graph 5.

On account of the alternating bands of light and shadow, the radiation received at any particular spot in the lath-houses during the course of the day is exceedingly variable. Measurements were made on clear days with a stop-watch photometer, the values for an entire day plotted on graph paper, and the radiation determined from the areas under the curves expressed in percentages of that for the sun station. It was found that the radiation in the five lath-houses was approximately 60, 35, 20, 10, and 5 per cent. of normal sunlight outside. Wind is of course greatly reduced in the lath-houses, even when a fairly strong breeze is blowing outside.

Holard tends to be higher in the lath-houses than outside, due principally to the reduced evaporation and transpiration. With proper attention to a watering schedule, the holard may be maintained at near the field capacity in all houses. The values obtained during the spring of 1940 are recorded in table 1.

No extended series of measurements of evaporation rates in the lath-houses have been made. However, a pair of Livingston white spherical atmometers operated for eight weeks in houses 10% and 35% showed that the evaporation rate in 10% was about 0.6, and in 35% 0.75, the value in the sun.

For the purpose of relating lath-house results to those in nature, use was made of a ridge of live-oaks (*Quercus agrifolia*) and of two large individual trees situated in the garden. These provided a range of light intensities approaching those under lath, but with temperature and humidity values of the out-of-doors (Plate 4B).

**In-and-out Huts.**—Since these habitats are essentially small lath-houses with approximately the same spacing between lath as in the large lath-house 10%, the factors are practically the same. Since measurements by recorders in the lath-huts 8' x 12' and 6' tall yielded results in agreement with those in the large lath-houses, an extension to the smaller in-and-out huts seems justifiable. However, records to verify this assumption are not available. (Plate 5).



**Dune Gardens.**—The control garden at Santa Barbara is ordinarily warmer during the day than the shelter garden, which in turn is warmer than the ridge, although the greatest difference (ridge to control) is seldom more than  $5^{\circ}$  F. The average daily minima at the ridge and control gardens are practically identical, while the shelter garden is definitely less than these, although rarely more than  $5^{\circ}$  F. below. In the 24-hour averages, ridge and control gardens are about alike, while the shelter garden runs about 1 to 3 degrees lower. (Plate 3).

In relative humidity the ridge garden has the highest values in both average and average daily minimum, while the shelter garden and control garden are progressively less. Ordinarily the extreme difference in average daily minimum (ridge to control) is less than 15 per cent. Graphs 1 and 2 show air temperatures and relative humidities for these three stations.

In wind movement the ridge garden has distinctly the highest values, the control garden the lowest, and the shelter garden intermediate. Occasionally, wind is sufficiently high to cause damage to vegetation in the exposed dune area, probably in large measure by sand blasting or scouring.

Radiation is practically the same for all three gardens, as indicated by both short-period measurements with a Smithsonian pyranometer (Abbot and Aldrich, 1916) and long-period values obtained from Livingston radio-atmometers. The reflected radiation from the sand at the dunes is a little greater, but this advantage is offset by the more frequent occurrence of fog in these situations.

Evaporation, whether determined by pan evaporimeters or by white spherical atmometers, is greatest at the ridge garden and lowest at the control garden, with the shelter garden intermediate, although the differences are small.

Soil temperatures at the two dune gardens are practically identical at all times, while in the 24-hour averages all three stations are alike. However, the average daily maximum at the control garden runs a few degrees higher than at the dunes and the average daily minimum a few degrees lower, but there is seldom more than  $10^{\circ}$  F. difference. This effect is due to the radiation characteristics of the soils in question, the loam at the control garden absorbing more radiation during the day-time and probably radiating more at night than the light-colored sands at the dunes.

In holard, the control garden has the highest values, at least in the top one or two feet, since the field capacity of the dune sand is only about 3.3 per cent of its dry weight. This value is the upper limit of holard for a considerable depth on the ridge, but in the shelter garden the water-table is nearly always within six feet of the surface of the soil, so that considerably more water is available to plants here than on the ridge and probably more than at the control garden, particularly to deep-rooted plants.

In fertility the control garden is definitely the highest, with the shelter-garden sand less, and the ridge sand nearly sterile. This relationship appears to be true for most of the species of plants employed in the studies reported here.

The question of salt-content of the sands in the dunes arises naturally on account of the proximity of these areas to the shore. Tests of the salinity of the ground water showed practically no salt-content, certainly not enough seriously to influence plant growth.

A more detailed description of these dune habitats is given by Martin and Clements in "Factors and Functions in Coastal Dunes" (1939).

## FUNCTION

### TRANSPIRATION

(Tables 4-8)

**Sealed Phytometers.**—For this series, plants of *Helianthus annuus* of a Canadian variety (S-490) were used. They were grown in cylindrical metal containers 8 inches in diameter and 10 inches tall, each fitted with a removable lid in the center of which was located a circular hole 2 inches in diameter through which the stem projected. For most of the habitats, these cans were filled with a sandy loam fertilized with approximately 20 grams of Vigoro to each can, but those for the two dune gardens were filled with sand from the particular area concerned and no fertilizer was added. Seeds were soaked in water for 24 hours, then planted at the rate of four to each can to permit some selection for uniformity, and allowed to germinate in the greenhouse. When the plants were large enough, the cans were sealed by placing a layer of plastic modelling clay over the opening in the lid and fitting it closely around the stem of the plant. If this clay is kept pressed closely against the stem, it effectively excludes water dur-

ing rains and reduces evaporation very greatly. In addition to this seal, the cans containing ridge sand had a layer of paraffin on top of the soil to reduce further the loss of water by evaporation from the soil surface. This extra precaution was not taken in the other habitats, since in these locations the plants grew sufficiently large that the loss of water by evaporation was an insignificant fraction of the total transpiration (Plate 9).

The seeds were planted February 10, 1940, the cans sealed and distributed to the proper habitats on March 4, and the plants harvested on April 22. These phytometers were weighed at least once each week, more frequently for the larger ones, and water was added in quantities sufficient to bring the holard back to the initial value. The frequency of weighing was determined by the requirement that the holard should remain well above the wilting range. The loam was maintained at near the field capacity (18% of the dry weight), and the sands at about 10 per cent of the dry weight.

The leaf areas of the plants were determined once each week by multiplying the product of length and width of the leaves by the factor 1.34 (Clements and Goldsmith, 1924), to yield the sum of both surfaces. The average leaf area during a week was assumed to be equal to the mean of the end values. The transpiration rates per unit leaf surface per day by weeks are given in table 4. These values fluctuate from week to week, due largely to variations in weather conditions, but partially to the gradual decline in rate with advancing age of the plants (Maximov, 1929). The ridge and shelter gardens exhibit practically identical average transpiration rates at 13.6 and 13.7 respectively, while the control garden at Santa Barbara is next highest at 9.8. The 8½-hour and 5-hour length-of-day sheds are only a little lower at 8.7 and 8.0 respectively, while the lath-houses show a decrease with reduced radiation to a minimum of 4.3 in lath-house 10%.

Near the end of this series, a short-period run was made, for two days in which the phytometers were weighed every two hours and the rates of transpiration calculated per unit leaf area. The results of this series are shown in graph 7. The points are located at the center of the time period between weighings, and clearly illustrate the diurnal march of transpiration. The average rates for the entire 12 hours are given at the right of the figure, and these indicate that there is little difference between rates at the ridge, shelter garden, and Santa Barbara sun stations. The plants in the 8½-hour shed also

average nearly as high a rate as those in the sun, while those in the 5-hour shed are only about three-fourths as great. This result is due to the fact that for the first two hours after removal of the 8½-hour sheds and for the last two hours before replacing them, the plants in this habitat had transpiration rates distinctly higher than the controls, while this effect was not noticeable in the case of the 5-hour shed. For the four hours around noon, plants in all three of these habitats gave practically identical rates. The only apparent explanation for this anomalous behavior is that during the first and last two hours of sunlight for the 8½-hour-day plants the transpiration rates of these plants are higher than that of the control plants because of the greater number of stomata per unit leaf area these plants possess. However, during the four hours around noon, they cannot maintain a rate greater than the control plants due to lack of water supply from the roots and consequent slight loss of turgor. This effect would not appear in the 5-hour-day plants, since they are exposed to the sun for only the four hours around noon. On this theory, the reduced-day plants would have higher transpiration rates at noon than the controls except for failure of an adequate water supply. This would require a smaller root system than really needed at times, and indeed the shoot-root ratio for these reduced-day plants is approximately twice as great as for the normal-day controls, lending some support to the hypothesis.

The rate of transpiration decreases in regular manner with reduced radiation through the series of lath-houses to a minimum in house 10% of approximately 0.4 that in the sun. This drop in transpiration rate is due largely to reduction in radiation, with very little effect from other environmental factors.

On April 22 the series was terminated, final measurements taken, the roots washed out of the soil by a spray from a nozzle, and the plants dried in an electric oven (Martin, 1934). The values obtained are given in table 5, and some are displayed in graph 8. The plants grown in the sun at the control garden at Santa Barbara are definitely the largest in the series in dry weight, leaf area, and total transpiration, and lowest in water requirement, while those at the ridge garden are smallest in dimensions and transpiration, and highest in water requirement. The extremes in total transpiration, per plant are 8410 grams for the controls, and 394 grams for those at the ridge. Water requirement values range from 120 grams per gram for the controls to 385 on the ridge. For the plants in the lath-houses the

range is from 258 gm/gm in lath 10% to 162 in 60%, constituting a regular series of increasing values with decreasing radiation. In the length-of-day sheds, the values are 259 for the 5-hour, and 183 for the 8½-hour. In this case also the water requirement increases with decreased radiation total.

Stem diameter, leaf area, and dry weight decline with reduced radiation from the control in the sun at Santa Barbara through both the length-of-day and lath-house series. Stem height is reduced in the length-of-day sheds, but reaches a maximum in houses 60%, 35%, and 20%.

An interesting comparison may be made between the plants in lath-house 20% and in the 5-hour length-of-day shed. In both habitats the plants had practically the same leaf areas, stem diameters, and dry weights, though the plants in lath-house 20% were nearly twice as tall but used only about three-fourths as much water. The plants in the 5-hour-day shed received about 3 times as much radiation total and were morphologically sun plants, but made a growth in dry weight equal to those in lath-house 20%, which were morphologically shade plants. Apparently, the sunflower can make better use of a certain amount of radiation if it is distributed over a longer period.

**Ecad Series Short-period Values.**—The method employed in these investigations consisted of cutting small shoots from plants growing in the various habitats, weighing them as quickly as possible on a "chainomatic" analytical balance, exposing them for a short time outside the balance and weighing again. Additional weighings were made at successive short intervals of time as long as desirable. During exposure to the physical complex, the shoots were held in an upright position by inserting the stem through a hole in a cork in a small jar. Weighings made at one-minute intervals for numerous species, indicated that the transpiration rate maintained a fairly constant value for from three to five minutes, even for thin-leaved plants. The length of time between weighings was taken as three minutes, since the loss of water during this interval was sufficient to permit accurate results on the analytical balance, but was not long enough for evidence of wilting to appear. Losses during the second three-minute period were usually less than during the first. Other writers have arrived at similar conclusions regarding the method (Stocker, 1929; Schratz, 1931; Oppenheimer and Mendel, 1939). Pfeleiderer (1933) has demonstrated that

the results obtained by this method agree very closely with those from plants growing in pots.

Rates of transpiration were calculated on the basis of fresh weight and also per unit leaf area. Measurements of the areas of the leaves were made by means of a photoelectric device of our own construction, but somewhat similar in design to one described by Kramer (1937). The area of only one side of the leaf was employed in calculations.

Since the principal desideratum was a determination of the relative transpiration rates of plants grown under different conditions, the method employed was as follows: the balance was placed on a sturdy table in the garden near the plants to be utilized and exposed to the sun in order that conditions for the shoots during and between weighings would be as nearly alike as possible. A shoot was cut from a plant in one of the habitats or eces under consideration, weighed on an even minute, and exposed to the sun on the table near the balance. A second shoot from a different habitat was cut and weighed on the next even minute of time, and similarly exposed to the sun. A third from still another ece was weighed on the third minute. On the fourth minute, the first shoot was weighed for the second time, and so on through the series as long as desired. Since it was necessary to weigh every three minutes, only three different shoots could be handled at one time. With very few exceptions, four such independent comparisons were made for a particular species in a given series of three habitats.

For the comparison of transpiration rates of shoots from different eces, those from a particular one of a given series were taken as a standard and the others were calculated with reference to it. The average ratios thus obtained are given in table 6.

Comparisons of the rates of transpiration of plants grown in the nutrient-water series show that for most of the species the plants in NW-0 have the highest rates and those in NW-2 the lowest, with NW-1 intermediate. The highest ratio observed, 4.40, was for the second three-minute interval of NW-0/NW-2 for *Mimulus cardinalis*. Most of the ratios were around 2.00, however. For two of the species, *Antirrhinum hispanicum* and *Oenothera trichocalyx*, no significant difference could be detected.

Similarly, the rates of transpiration of shoots from plants grown in lath-houses 10% and 35% are usually greater than those from the sun group NW-2. The maximum ratio observed in this series was

4.05 for LH 10%/NW-2 in the second three-minute interval with *Mimulus cardinalis*. For the in-and-out huts, which are essentially sun and shade habitats, the ratios were less than unity, the shade shoots (In) having lower transpiration rates than those grown in the sun (Out).

Comparisons of ridge and shelter garden plants exhibit little difference in some cases, and in a few the ridge plants possess slightly lower rates. In the case of the soil-pits, the plants in sand and adobe exhibit rates somewhat higher than those in the loam, the maximum ratio observed being 1.72 for adobe/loam during the second three-minute interval with *Mimulus cardinalis*.

In the length-of-day series, there is no significant difference among the various groups for *Antirrhinum hispanicum* and *Verbena prostrata*, but in *Mimulus cardinalis* the reduced-day plants show rates a little greater than the normal-day ones, the maximum ratio observed being 1.52 for short-day/long-day in the first three-minute interval.

For the competition series, the plants with 4 and 16 individuals per square meter show little difference in transpiration rate, while those in the 64 or denser plots in general run appreciably lower, the lowest ratio observed in the first three-minute period being about 0.4 in the cases of *Arctotis grandis* and *Rudbeckia bicolor*, both for the 64/4 groups.

In both the nutrient-water and soil-pit series, the smaller plants have the highest transpiration rates, with a few exceptions in which there is no appreciable difference. In the competition groups, however, the relationship is just the opposite, the smaller plants showing lower rates. The explanation of this phenomenon appears to lie in the relation of the plants to the water-content of the soil during the growing period and the resulting growth and behavior of the plants. For the nutrient-water series, the plants in all beds were equally spaced, with the result that competition for water was probably greatest in the NW-2 group, even though the holarid was practically the same in all three groups. Consequently any effect of restricted soil moisture in reducing transpiration rates would appear in this group. Frequently, plants grown in less favorable conditions have more stomata per unit surface, and the leaves are more openly exposed to the circumambient factors. For these reasons, the smaller plants of a species might be expected to show higher transpiration rates than the larger individuals. In addition to these factors, there probably is a relationship between

the size of the leaves and their rate of water loss similar to the one pointed out by Leighly (1937) for evaporation from free water surfaces, in which case the small leaves of a given species would be expected to have somewhat higher transpiration rates than large ones, other factors being the same.

In the competition series, the small plants in the more densely planted plots have lower rates of transpiration than the large ones in the quadrats with 4 and 16 individuals per square meter. In this case the contradictory behavior is probably due to the fact that there is considerable competition for water in the denser plots, with the result that these plants have developed means for reducing transpiration rates. Whether this protection against water loss is developed in the cuticle, number of stomata per unit area, in the vascular system, in some other plant character, or in some combination of these is conjectural.

In the soil-pit series, the small plants grown in adobe and sand have higher rates of transpiration than the larger ones in loam, although the ratios are not so high as those obtained in the nutrient-water series. In the case of the sand, soil moisture is low, but apparently is not sufficiently limiting that its effect can overcome the factors in favor of a higher rate of transpiration in the smaller leaves.

Since the plants of the ridge garden have smaller leaves than those at the shelter garden, they would be expected to show higher transpiration rates. However, the opposite is usually true, and the cause is probably the reduced water supply on the ridge.

Plants from the shade exhibit relationships similar to those of plants grown in the sun. Those in the large lath-houses were all equally spaced so that any effect of competition for water would decline with decreasing radiation. These plants have a much more abundant supply of water than those in the sun and consequently would be expected to develop little protection against water loss. Ordinarily, shade forms have a less well-developed cuticle and are a darker green color than sun forms. Both these factors tend to increase transpiration rates in the one as compared with the other, especially when both are exposed to full solar radiation.

For the in-and-out series, the shade forms have lower rates of transpiration than the sun forms, a behavior just opposite to that of the individuals in the large lath-houses. Possibly the explanation of this anomaly lies in the fact that both forms of the in-and-out group



are on the same root system, with the result that the shoots in the sun take a large fraction of the available water and thereby create a deficit in the shade portions of the plant. If this be the case, the shade leaves would develop a resistance to water loss similar to that shown by the competition groups.

The reduced-day plants are morphologically sun plants, but are usually smaller than normal-day plants. Since the spacing was equal for all groups, the small plants did not suffer from water shortage, and consequently their response was much the same as that of plants in the nutrient-water group.

*Antirrhinum hispanicum* and *Oenothera trichocalyx* show very little difference in rate of transpiration, regardless of the habitat in which they were grown. On the other hand, *Mimulus cardinalis* exhibits great variability, the maximum ratio observed being 4.40. Evidently there is no universal rule for response of species to environment, at least as far as rate of transpiration is concerned. Most species, however, respond to a high degree, others very little.

In order to determine the behavior of the transpiration rates of cut shoots during wilting, some of the weighings were continued for as long as 24 minutes. The results of these measurements are given in table 7, and some are presented in graphs 9 and 10. In the table, the upper values for each shoot represent the rate of transpiration in grams per square decimeter of leaf area per hour, while the lower ones are the fresh weights of the shoots in per cent. of the initial value. The rapid decline in rate after the first three-minute period is at once apparent; in some cases the rate falls to one third of its initial value in fifteen minutes. Visible wilting usually occurs within the second three-minute interval.

The values for relative fresh weight demonstrate that most of the species are able to withstand a loss of only about 3 to 5 per cent. before the transpiration rate is affected. However, *Antirrhinum hispanicum* maintains its rate until nearly 10 per cent. of the fresh weight has been lost. Visible wilting occurs in many of the species after a loss in fresh weight of only 3 per cent.

Transpiration rates were calculated on the basis of fresh weight, and some of them are recorded in graph 11. Since a comparison of the values for plants from different habitats disclosed that the ratios differed but slightly from those calculated on the basis of leaf area, they have not been included in the tables of data.

The rate of transpiration per unit leaf surface or per unit fresh weight is only a part of the question of adaptation of a plant to its environment. The transpiration per plant is also of importance, since the total amount of water a plant uses is determined at least partially by the amount available in a given habitat. In order to calculate the relative amounts of water transpired per plant in the various habitats, the relative total leaf areas of typical plants were calculated, and these values were multiplied by the relative transpiration rates per unit leaf area. Since *Mimulus cardinalis* showed the greatest variability in the transpiration rate of all the species, it was selected for this purpose, and the values obtained are given in table 8. The plants in the nutrient-water series all transpire approximately equal amounts of water, even though the ones in NW-0 have only about 0.3 the total leaf area of those in NW-2. This is readily explained by the fact that the former have a transpiration rate nearly three times as great as the latter. Plants in the lath-houses use less water than those in the sun and those in adobe less than in loam. Medium-day plants lose more than the long-day ones, while the short-day plants transpire less.

These relations are not true for all the species, since the relative leaf areas are in roughly the same ratios as for *Mimulus*, while the transpiration rates are more nearly equal. Consequently, the general rule is that the smaller plants transpire less than the large ones.

#### FORM

(Tables 9-13)

#### PHYTOMETERS

**Helianthus Annuus Series I.**—In the growth series, free phytometers of a Canadian s-490 variety of *Helianthus annuus* were used. They were obtained from seed germinated in the greenhouse in cylindrical tar-paper pots 2 inches in diameter and 9 inches tall, containing soil of the type in which the plants were to be grown. The seeds were soaked in water for 24 hours, then planted on February 10, 1940, and transplanted to the gardens about two weeks later at the rate of 64 plants to each habitat. The plants were harvested at the rate of 8 each week for a period of eight weeks for a determination of the rate of increment in dry weight in the various situations. The values obtained are given in table 9. The dry-weight increments fluctuate considerably, partly due to variations in weather factors

from week to week, and partially on account of statistical differences among individuals of a given group. On the average, the dry-weight increments for the various eces bear the same relationship to each other as exists among the final dry weights obtained on April 29. Consequently, it is sufficient to limit the discussion to the latter values.

The plants grown in the NW-2 habitat were the largest in the series in leaf area, stem diameter, and dry weight. Those in NW-0 were about half the size of these, while the ones in NW-1 occupied an intermediate position. The individuals in loam were about two-thirds the size of the largest ones, with those in adobe and sand at about 15 and 1 per cent. respectively. The values obtained in the lath-houses form a regular series, decreasing with reduced radiation to a dry weight in house 10% of only about 1 per cent. of NW-2.

The shelter-garden plants are much smaller than those in NW-2, while those at the ridge are the smallest in the series, with a dry weight average of only 0.35 grams, as compared to 72.4 grams for the largest plants. These figures illustrate very effectively the relatively great range of growing conditions in the adaptation gardens.

In the series in the sun, stem heights fell in the same order as dry weights, although the differences were smaller. The plants in most of the lath-houses, however, were taller than those in the sun, the maximum height occurring in houses 60% and 35%. Plants in lath-house 10% were somewhat shorter than those in the sun, NW-2. These results are in good agreement with those reported by Clements and Long (1934, 1935) in their studies of factors concerned in growth and elongation of plants under different degrees of radiation and holard.

Calculations were made of a faculty of these plants that we choose to call the "growth rate," which is identical with "net assimilation rate" as defined by Gregory (1926). It is the dry weight of plant material produced per unit leaf area during a given interval of time. The values obtained from the present series were found by dividing the increase in dry weight over a period of nine weeks (from transplanting to harvesting) by the average leaf area during the nine-week period. The average leaf area for a particular set of plants was found by dividing the difference between the initial and final leaf areas by the difference between their natural logarithms. This formula is the one used by Gregory (1926) and rests upon the assumption that the leaf area of a plant is an exponential function of time.

The values of growth rate for *Helianthus annuus* in the various habitats in the adaptation garden are given in table 10, and are illustrated in graph 12 (8B). In the nutrient-water series, it ranges from 0.706 grams per square decimeter per week in NW-2 to 0.539 in NW-0, with NW-1 intermediate. The value in loam is 0.556, in adobe 0.356, and in sand 0.156. At the ridge and shelter gardens, the values are 0.158 and 0.292 respectively. The lath-houses constitute a regular series, the growth rate falling from 0.362 in house 60% to 0.070 in 10%.

The maximum value observed was 0.706 in NW-2 and the minimum 0.070, in lath house 10%, the former being approximately ten times the latter, a result that is not in accord with Gregory's conclusion that the "net assimilation rate" for a given species is approximately the same regardless of environment.

The results from lath-house 35% and from NW-0 provide an interesting comparison of the differences in the behavior of sun and shade plants of a given species. The final leaf areas of the plants in these two habitats were nearly equal, but those in the lath-house had only about half as much dry weight, with the result that their growth rate was only about half as large. The plants in the shade tend to produce a larger leaf area in proportion to the dry weight than do sun plants.

**Helianthus Annuus Series II.**—Since the above values of growth rates were obtained from relatively few plants per set and with a long time interval, an additional trial was made, employing more plants and taking measurements each week. This series was started at the same time as series I above, using similar seed and methods. A group of 150 plants was transplanted to each of five habitats, lath-house 20%, NW-0, NW-1, ridge garden, and shelter garden. Measurements of leaf area were taken each week and 25 plants were harvested for dry weights. The same procedure as for series I was employed to obtain growth rates, and the values are given in table 11. These exhibit a fair amount of fluctuation from week to week, partly due to statistical variations among individuals in a given set and partly on account of environmental changes. Since the dry weight of a particular set was taken as the initial dry weight for the succeeding one, statistical variations among individuals become important.

These values of growth rates are in good agreement with those

obtained in series I. The average of the five weekly values for the NW-1 plants was 0.421, for NW-0, 0.391, and for lath house 20% it was 0.170, while the shelter and ridge gardens gave values of 0.271 and 0.147 respectively. In this case the largest value was only three times the minimum.

The plants in lath-house 20% produced nearly three times as much dry weight as those at the shelter garden, but had a growth rate only about 0.6 as great. This effect was due to the relatively large leaf area of the plants in the former habitat, the final area being approximately 7 times as great as in the latter case.

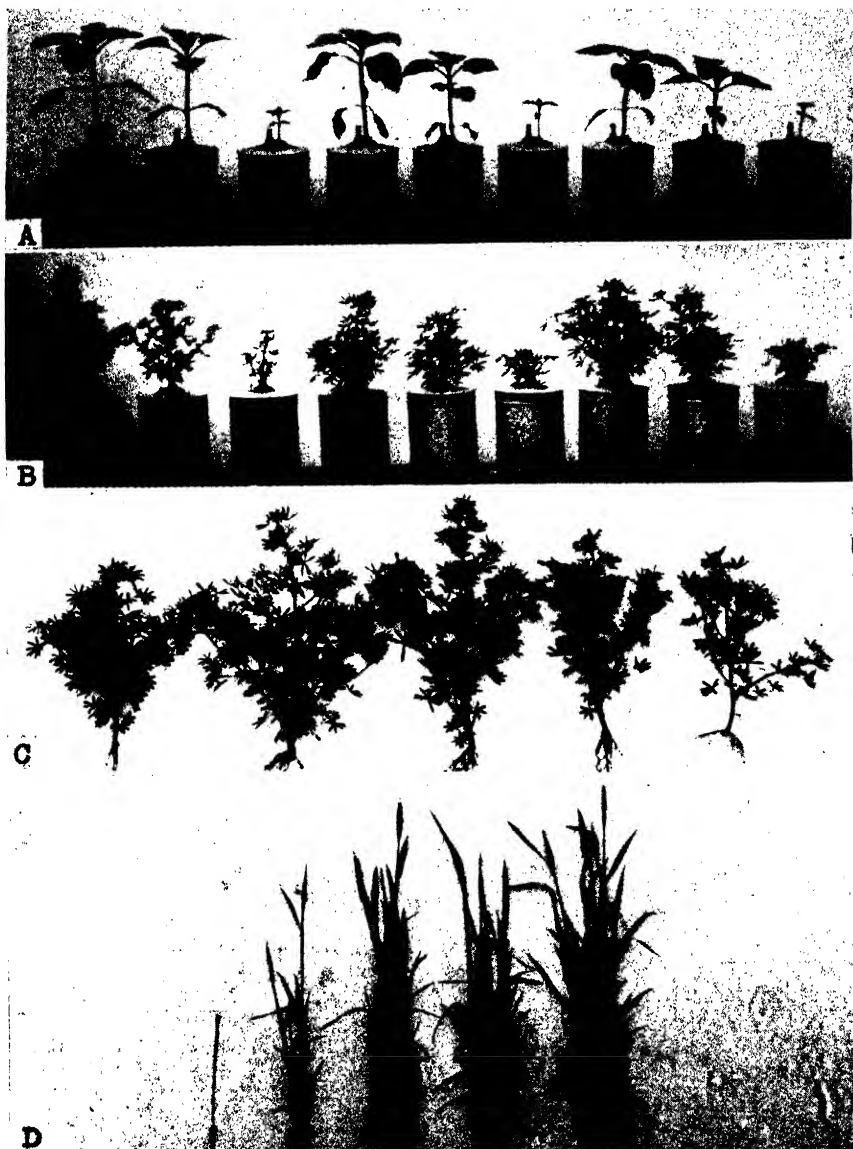
#### PHYTOMETERS AS STANDARDS

The comprehensive series of sealed and free phytometers was installed to analyze the functional and structural responses to the stable dunes in the shelter garden, and the mobile dunes of the ridge garden along the seashore, and to compare them with the results obtained in the main garden further inland.

The results show that stem height is the best indicator of growth conditions in the three soils, as well as in the corresponding gardens. Stature decreases consistently from garden loam to stable and mobile sand in practically seven replications, as it does likewise, though to a smaller degree, from the main garden to the shelter and ridge gardens. Transpiration and dry weight behave in the same fashion; the former varies as 50:20:2 in the three soils: loam, adobe and sand, and as 6:5:4 for loam in main, shelter and ridge gardens. In general, the water-requirement falls from mobile to stable sand, and from ridge to shelter to main garden.

Lupine phytometers are in accord as to the reduction of stature, transpiration and dry weight, from loam to mobile sand, but as to gardens, the dry weight was highest in the ridge and lowest in the main garden, a departure probably to be explained by the fact that this is typically a dune species. However, when the whole plant was exposed to dune conditions, as in the free series, lupines gave values of 44, 24, and 4 gm. from loam in the main garden to mobile sand on the ridge. Where flat pans were placed at such depth in the sand as to prevent water from sinking below the root level, the stature was one-fourth as great and the weight three times greater for both sands than in the control. The addition of fertilizer to the loam had but

# PLATE 9



## Phytometers.

- A. Sealed *Helianthus annuus* phytometers: Loam, Shelter-garden sand and Ridge sand in order from left to right, for each of the three gardens: Main, Shelter and Ridge.
- B. Sealed *Lupinus chàmissonis* phytometers, same as in "A."
- C. Free lupin phytometers in Main Garden (left to right): 1. Ridge sand; 2. Shelter-garden sand; 3. Loam, watered; 4. Loam, rain only; 5. Loam, fertilized and watered.
- D. Free *Triticum sativum* phytometers as in "C."

little effect, while in both stable and mobile sand it increased growth several times (Plate 9).

### CORRELATIONS

**Soils and Nutrients.**—The behavior of more than 100 adapted species was in close agreement with the phytometers as to stature, leaf-area, dry weight, size and number of flowers, etc. Contrary to the usual view, such aerial factors as wind, humidity and temperature have proved to be of much less importance than water-content and nutrients. The mobile sand is lowest in these two factors and hence constitutes the most xeric situations. Most species are unable to maintain themselves in it, and those that do so are strikingly dwarfed. This is due primarily to the rainless season of six months or more, although the addition of fertilizer is much more effective than water in stimulating growth, the ratio being about 10:1. However, much of this is owing to the fact that the latter passes beyond the root layer so that the hoiard approximates 3% since the pan results show that water may be equally effective. It is probable that the fertilizer acts chiefly by promoting a better root-system which is able to draw water from a much larger mass of soil (Plates 10-17).

Dune sand is one of the most effective agents for bringing about the inversion of habitats without destroying the plants originally present. An instance of rapid and extensive evolution of this type occurs in nature on the California Coast, where high winds have swept the sand well up the slopes to produce a new habitat, with corresponding modifications of the dominant species to the number of 25 or more. These forms are for the most part, the dwarf-procumbent type produced by the joint action of strong wind and low water and nutrient content (Plates 18-20). These factors express themselves in a recurring series of small differences, with the result that most of the species exhibit a continuous line of ecads, indicating that adaptation operates to produce new forms without the intervention of natural selection.

In the experimental gardens, species transplanted to the dunes, show the highest osmotic concentrations. Survival is much the lowest in shifting sand, and only a few species, mostly shrubs, are able to pass successfully through the long dry season. Annuals show a much lower mortality in stable sand, while perennials that persist through the first year, usually become permanently established. In some cases,

at least, this is due to the ability of the roots to follow the retreating water-table of the rainy season downward from the 1-foot to the 6-foot permanent level. The general conditions are favorable to the accumulation of woody tissue, and a number of annuals have developed into evergreen half-shrubs. This is in accordance with the high survival noted for transplanted shrubs.

**Lath-houses.**—The thoroughgoing discussion of the factors functions and growth effects as shown by phytometers in sun and shade habitats, serves as a standard for the comparable results in the degrees of sun and shade in the several lath-houses (Plates 21, 22C). For the purpose, however, of relating these plants to natural habitats, 27 species, mostly annuals, were sown in transects running from deep shade beneath trees of live-oak (*Quercus agrifolia*) in the main garden, through half-shade to full-shade (Plate 4B).

**Oak Transect.**—Growth, form and flowering in this transect, with average light intensities for the three sections of the transect of 5%, 20% and 100%, were naturally influenced by the normal habitat of each species. Species such as *Nemophila aurita* for instance, endured deep shade better than those of sunny habitats, while, on the other hand, xeroid species such as *Mentzelia aurea*, grew best in the sun, nearly as well in half-shade, but poorly in full shade. The majority of species made the best growth in half-shade and fell off toward both extremes of light. The mode was graphically exhibited in the transect for each species, the curve of height rising gradually from that in the densest shade, represented as "zero," to 2 to 4 times in the half-shade and then falling to zero again at the edge of the sun area. Size and number of leaves and flowers as well as color and pubescence, were closely correlated with height. Shade species, such as *Nemophila*, yielded a maximum in dense shade, and the curve fell to zero in the sun, while *Mentzelia* gave just the inverse curve. *Stipa setigera* produced panicles only in the middle or half-shade third, the height falling off equally toward both extremes (Plate 22 A,B).

**Length-of-day Series.**—In attempting to disclose the factors involved in seasonal aspects and in the annuation of dominants and subdominants, often strikingly exhibited under a winter rainfall, the length-of-day tents have been used in a series of a long-day of 14 hours exposure to sunlight, mid-day exposures of 10 hours and a short-day exposure of 5 hours. These series are also designed to afford an



interpretation of the flowering behavior of alpine and plains species. In the transplant gardens, the former in particular have been led to bloom in practically every month of the year, partly in the Alpine Laboratory and partly at Santa Barbara, with no evident relation to the length of day.

Approximately 50 species grown in the tents have exhibited much the same relation found in the lath-houses with the light intensity reduced to 12% and 4% of normal sunlight. The long-day cultures, i.e., the controls exposed throughout the day, regularly flower first and at a lower stature. The medium-day ones, with an exposure of 10 hours, flower two weeks later and at the greatest height, while the short-day series flower 2 weeks later still or not at all, under an illumination of 5 hours. Again, as with the shade series, this is essentially an energy relation, as indicated by dry weights and combustion values.

For such vigorous genera as *Clarkia* and *Verbesina*, growth was best in the full-day, while low delicate forms, such as *Nemophila insignis* and *Phacelia campanularia*, grow best in the medium-day row. The latter yielded the most striking modifications, the plants of the mid-day being greatly suppressed, with very short nodes, fleshy stems, large leaves and elongated petioles forming definite rosettes. The short-day plants exhibited the same characteristics but to a smaller degree. The form was almost exactly that of a typical strand plant, and suggests that more diffuse illumination may be a factor in the production of the latter (Plates 23-25).

**Competition Cultures.**—Fifteen of the same species as were grown in the oak transect were also sown in competition cultures, each with a density of 4, 16, 64 and 256 to their respective quadrats (Plate 7). The average light intensities for the three sections of the transect were 5%, 20% and 100%, and those in the competition plots ranged from 4% in the quadrat with 256 plants to 7% in the 64's, 15% in the 16's, and 100% in the 4's, while the water-content increased in the same direction. Concordant results in every respect were obtained in these two experiments and these were also in harmony with the extensive series of such experiments in Lincoln during a period of four years. (Clements, Weaver & Hanson, 1929).

The average height of *Mentzelia aurea* decreased in the same sequence from 32, 26, 24, to 22 inches, and the width increased from

10 to 21 inches. The suppressed individuals in the 256 quadrat averaged 8 inches tall and 2 mm. in stem diameter, in contrast to 32 inches and 15 mm. for the dominant ones around the edge. They were mostly 1-2-flowered and the flowers averaged less than one-third the size. The behavior was consistently the same in the other cultures (Plates 26-29).

Under the stimulus of drouth (or competition), three species of *Phacelia* have yielded striking results. Two related species, *whitlavia* and *parryi*, have produced new forms more unlike the parent in all respects than the two species are unlike each other, while the third, *grandiflora* has re-developed into a form little different from *viscosa*, thus confirming Gray's view that the former is merely a variety of the latter (Plate 30).

The photographs that illustrate the preceding discussion of the correlations between factors and form, follow in an uninterrupted series of plates (10-34). Tables 12 and 13 present further data in the record of measured changes in form in response to the factors of the habitat.

PLATE 10



*Helianthus annuus.*

A. Nutrients: 1. NW-2; 2. NW-1; 3. NW-0.

B. Soils: 1. Loam; 2. Adobe; 3. Sand.

PLATE 11



Transplants from Main Garden to Dune Gardens.  
A. Series in Ridge Garden; right row treated with vigoro.  
B. Two plots in Shelter Garden: *Chrysanthemum* and *Godetia*.

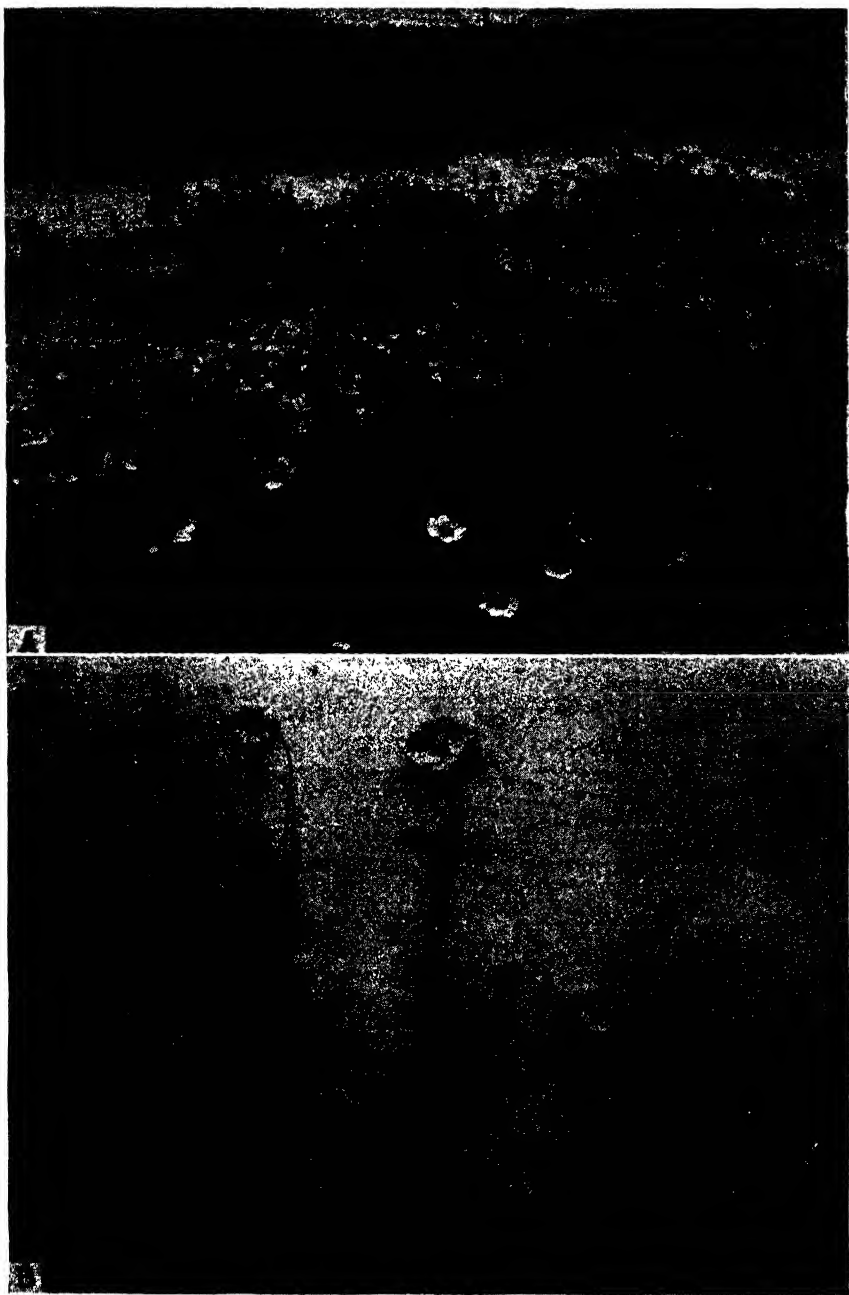
PLATE 12



Adaptations of *Antirrhinum hispanicum*.  
(TABLE 13)

- A. Transplant plot in Dune Shelter Garden.  
B. Ecads: 1, Main Garden; 2, Shelter Garden; 3, Ridge plot, fertilized;  
4, Ridge plot, not fertilized.

PLATE 13



*Coreöpsis lanceolata grandiflora.*

A. Transplant in dune Shelter Garden.

B. Adaptation forms: 1. Main Garden; 2. Shelter Garden; 3. Knoll Garden.

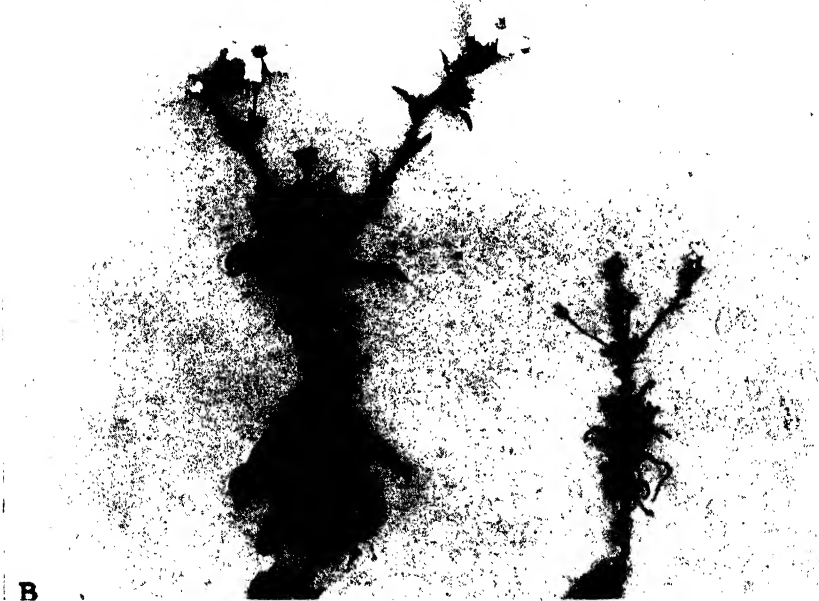


Adaptations in Dune Gardens.

- A. *Agoseris heterophylla*: 1. Main Garden; 2. Shelter Garden; 3. Ridge Garden.  
B. *Phacelia whitlavia* (Table 13): 1. Shelter Garden; 2. Ridge Garden.



A



B

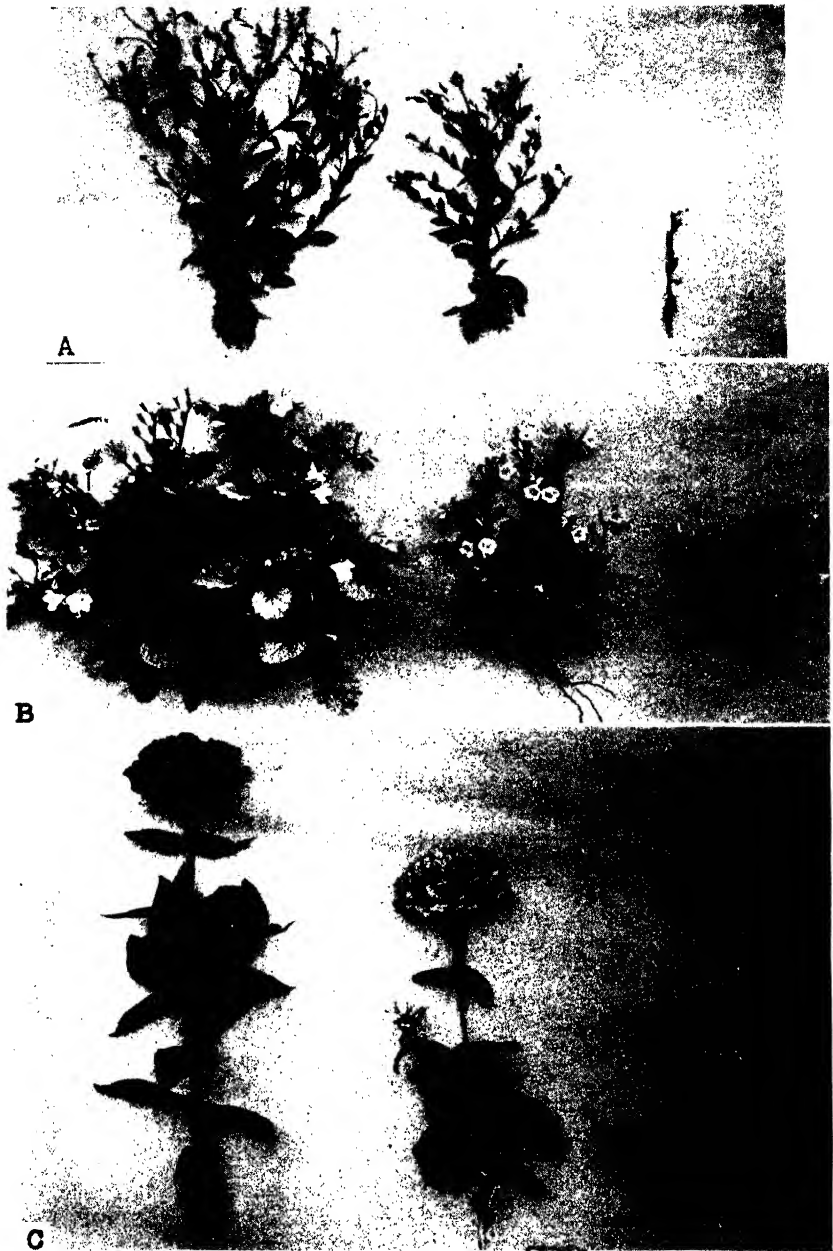
Ecads of *Madia elegans*.  
(TABLE 13)

A. Soils: 1. Loam; 2. Adobe; 3. Sand.

B. Dune Gardens: 1. Shelter Garden; 2. Ridge Garden.



PLATE 16



Adaptations to Soils: 1. Loam; 2. Adobe; 3. Sand.

(TABLE 13)

A. *Rudbeckia amplexicaulis*

B. *Phacelia campanularia*.

C. *Zinnia elegans*.

PLATE 17



A



B



C

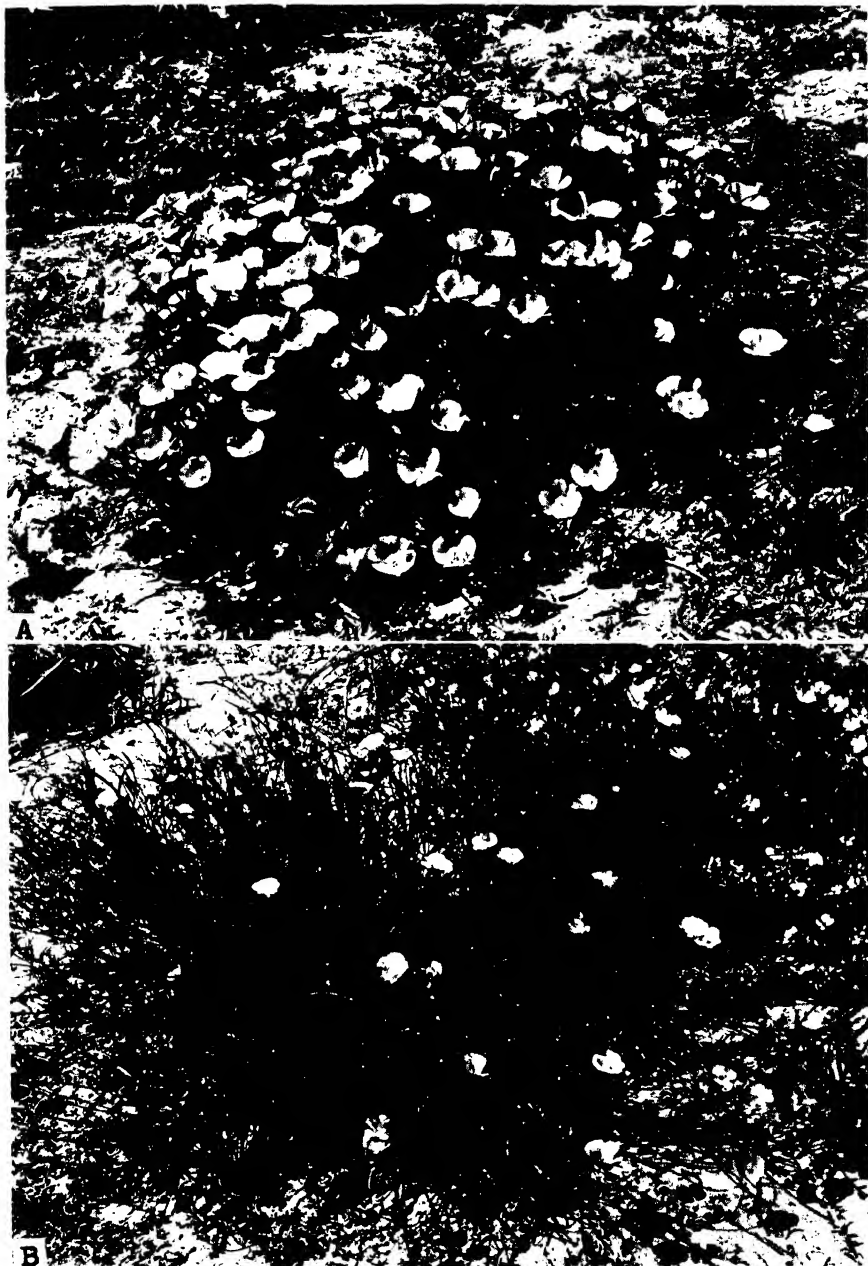
Adaptations to Nutrients. 1. NW-2; 2. NW-1; 3. NW-0.  
(TABLES 12-13)

A. *Mimulus cardinalis*.  
B. *Antirrhinum hispanicum*.  
C. *Oenothera tricalyx*.

PLATE 18



Prostrate Forms in Sand Dunes.  
A. *Lotus scoparius*: Coast dunes.  
B. *Franseria bipinnatifida*: Shelter garden.  
C. *Oenothera spiralis*: Ridge garden.



*Eschscholtzia californica.*

- A. Volunteer in Shelter Garden, with dense, erect stems, large orange-colored flowers, and large torus.
- B. Native spreading decumbent form on slope of dune, with small yellow flowers and small torus.



A



B

*Eschscholtzia californica*: A. 1. Erect volunteer; 2. Procumbent form.  
B. 1. Normal plant from Main Garden; 2. Climber in dune shrub.



Adaptations to reduced light: (TABLE 13): 1. 100%, 2. 65%, 3. 44%, 4. 27%, 5. 11%  
A. *Madia elegans*; B. *Antirrhinum hispanicum*.



Adaptations to Shade.

A. *Salvia argentea*: 1. Main Garden; 2. Shelter Garden; 3. Oak transect.

B. *Digitalis gloxinoides*: (As in "A").

C. *Solanum douglasii*: 65%; 44%; 27%; 11%; 5%.



Length-of-day and In-and-out Experiments.

A. *Trifolium pratense* plots (left to right): 1. Long-day; 2. Mid-day;  
3. Short-day.

B. Short-day *Trifolium* from In-and-out hut.

C. *Clarkia pulchella*: 1. Out-and-in; 2. In-and-out.





Length-of-Day: *Matthiola incana*:

- A. Plots in Main Garden (right to left) : 1. Long-day; 2. Mid-day; 3. Short-day.  
 B. Individuals from plots (left to right) : 1. Fertilized control; 2. Long-day;  
 3. Mid-day; 4. Short-day.



Length-of-day: *Triticum sativum*:  
(TABLE 13)

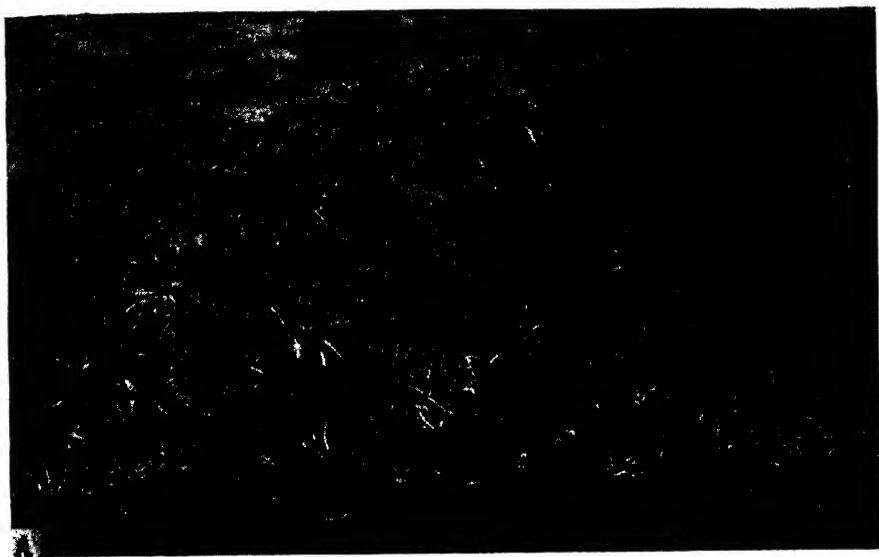
- A. Plots in Main Garden (right to left) : 1. Long-day; 2. Mid-day; 3. Short-day.  
B. Individual from plots (left to right) : 1. Long-day; 2. Mid-day; 3. Short-day.



Competition.

A. Plot of *Papaver rhoeus*.

B. Individual plants from bed showing degrees of competition.



Competition in *Matthiola incana*.  
(TABLE 13)

A. Plot in Main Garden.

B. Individuals from plot: 1. Corner; 2. Side; 3. Center.



Competition Forms.

- A. *Viola nigra*: Normal, open ground form, and two plants dwarfed by crowding.  
 B. *Encelia californica* plants representing degrees of competition in "La Jolla" dunes.  
 C. *Chrysanthemum coronarium* series in loam and Ridge Garden sand.



Competition Forms.  
(TABLE 13)

- A. *Arctotis grandis*: 1. Corner; 2. Margin; 3. Center.  
 B. *Phacelia tanacetifolia*: 1. Open ground; 2. Weed-group; 3. Family-group;  
 4. Suppressed.  
 C. *Chrysanthemum coronarium*: 1. Plant from center of loam bed in Shelter  
 Garden (See Plate 32); 2. Normal form in Shelter Garden.



*Phacelia whittlavia.*

(TABLE 13)

A. Adaptation to Soils: 1. Loam; 2. Adobe; 3. Sand.

B. Conversion to *parryi* in late-season, drying soil of Wild Garden.



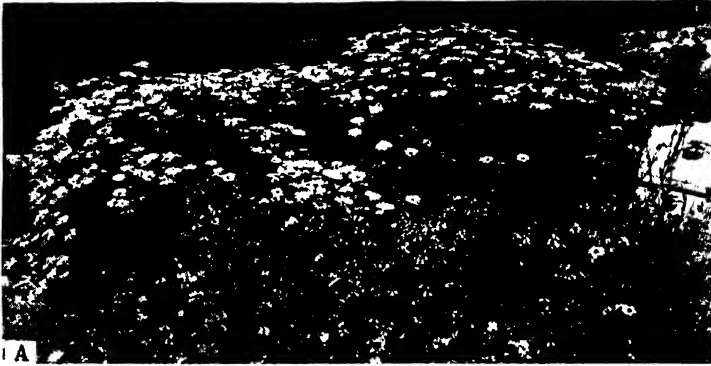
Adaptation Forms of *Phacelia grandiflora*.  
(TABLE 13)

A. Nutrients: 1. NW-2; 2. NW-1; 3. NW-0.

B. Soils: 1. Loam; 2. Adobe; 3. Sand.

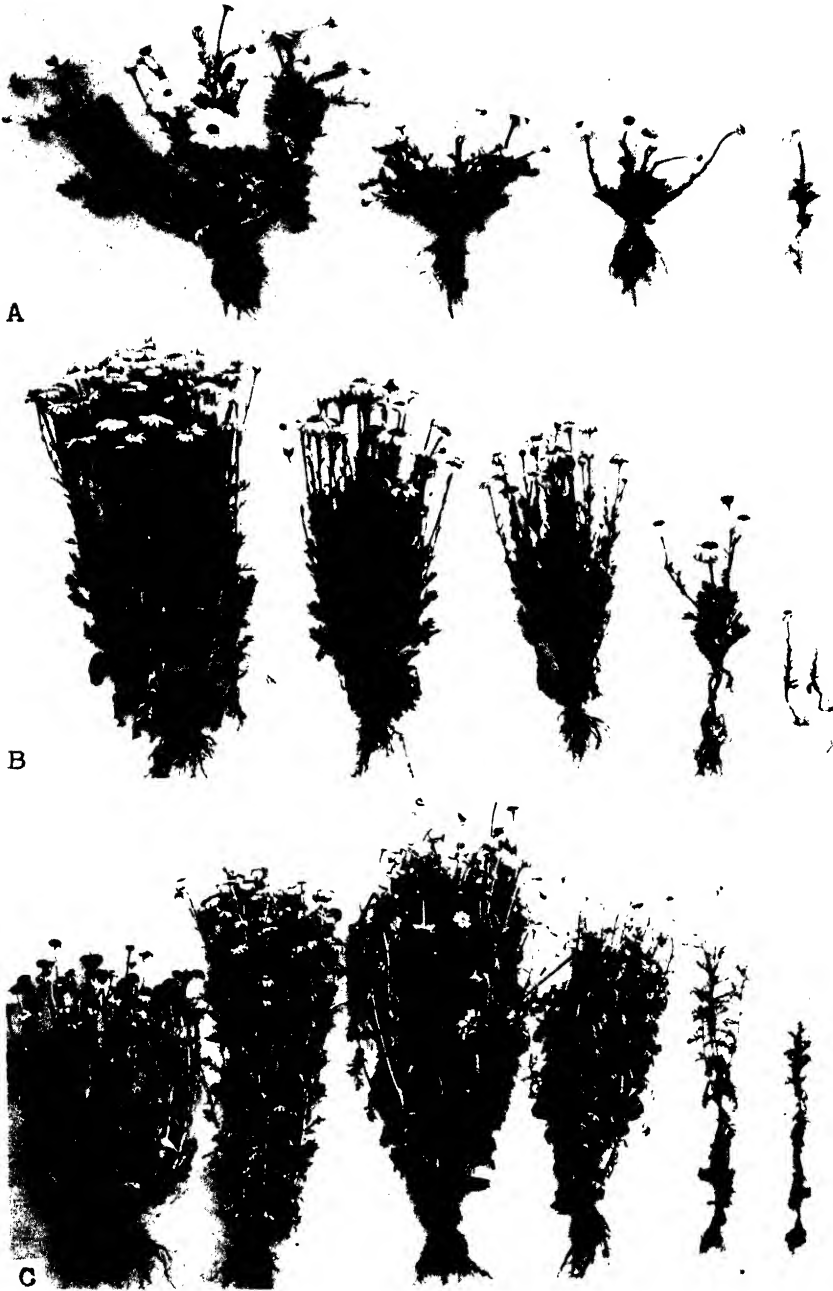
C. Length-of-day: 1. Long-day; 2. Mid-day; 3. Short-day.





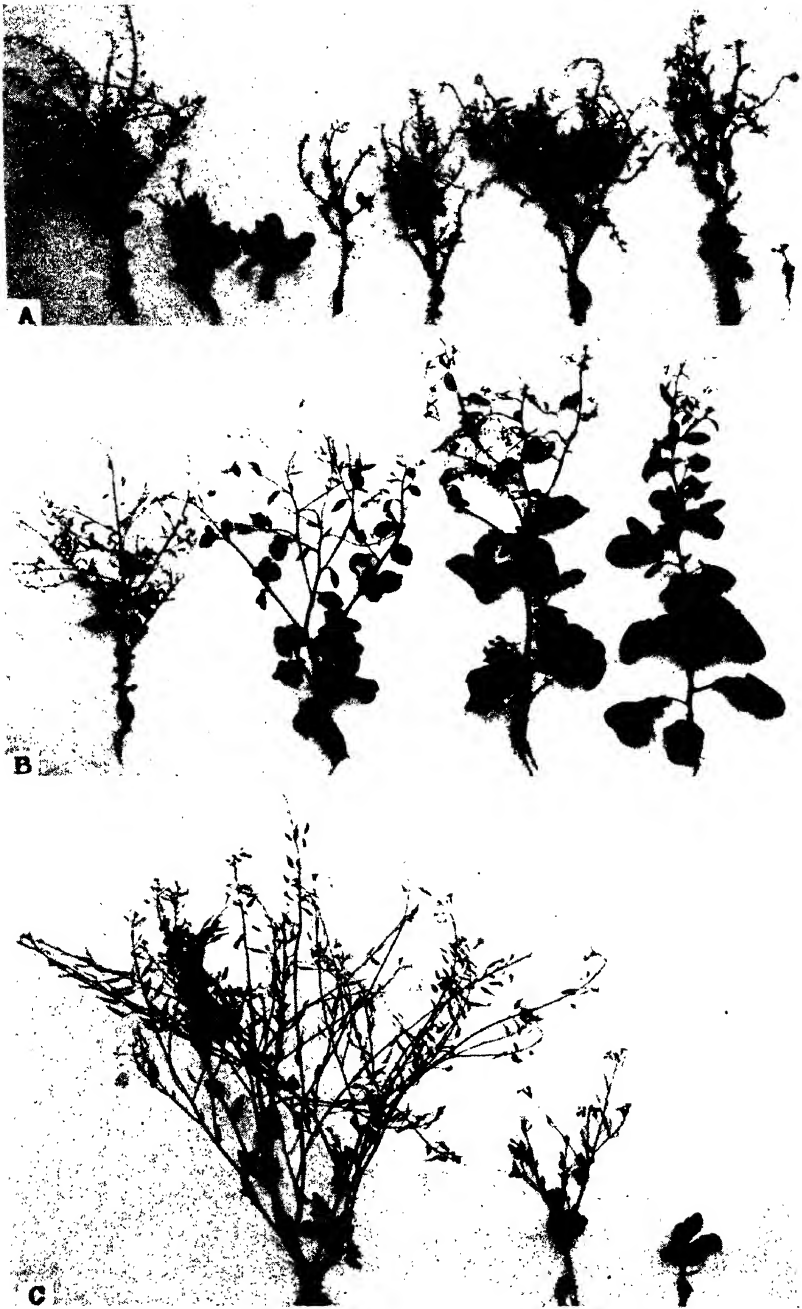
Adaptations of *Chrysanthemum coronarium*.  
(TABLES 12-13)

- A. Competition bed in Shelter Garden loam.  
B. Length-of-day: 1. Long-day; 2. Mid-day; 3. Short-day.  
C. Soils: 1. Loam; 2. Adobe; 3. Sand.



*Chrysanthemum coronarium* (TABLE 13): 1. Shelter; 2. Knoll; 3. Ridge, fertilized; 4. Ridge, not fertilized. B. Nutrient & Garden Series: 1. NW-2; 2. NW-1; 3. NW-0; 4. Shelter; 5 & 6. Ridge. C. Sun and Shade Series.

PLATE 34



Adaptations of *Raphanus sativus* (TABLE 13).  
A. 1-3. Length-of-day Series; 4-6. Nutrient Series; 7. Shelter; 8. Ridge.  
B. Light Series; C. Soil Series.

## CHAPTER III

### BEHAVIOR

The sequence of events within the green plant is ushered in by the impact of such direct factors as water, light, heat, and nutrients, upon the protoplasm in its various forms. These immediately set in operation the simpler functions, which are then integrated in photosynthesis and chemosynthesis. With little or no delay, the latter pass to the threshold of the complex known as metabolism, out of which arise the phenomena of growth and behavior. No distinct line can be drawn between these, especially when the tropisms are taken into account, but in general, growth is to be regarded as the increment of mass and weight. It may be distinguished as primarily quantitative; by contrast, behavior is qualitative in essence.

This series of functions constitutes an interwoven pattern of rhythms, both large and small, single and combined. The typical aspect is displayed under the normal rounds of factor stimuli, daily, seasonal, and yearly, in which a certain range of fluctuation is inherent, except under the most rigorous control. When a factor change beyond this impinges upon plant or organ, the existing rhythm is disturbed for a time, while an adjustment takes place. Following this, the normal cycle is usually resumed, but on a different level. The new phase extends throughout the dynamic system of the plant, but can be followed best in its visible or measurable manifestations. That these are represented by immediately antecedent causal alterations in protoplast and tissue can hardly be doubted. It is in these intimate biochemical processes that the proximate causes of transformation, of adaptation and fixation, must be sought. However, in the present treatise, attention is directed to the tangible functions and changes, chief among them those of growth, behavior, and form, though the exploratory experiments in correlation do represent a gross attack upon the biochemistry of the various protoplasts.

**Kinds of Rhythm.**—The reproductive rhythm has been the one chiefly studied, and the flowering phase of this. Fruiting and seed production have been necessary features of the approach to acclimatization and ecesis; together with rootstocks and buds, they represent the storage aspect of the food cycle. Modification through manipulation

proceeds from changes in the nutrition stream, while the direct factors of the habitat or *ecce* alter the flow or direction of this to affect growth, behavior, or form. In this is involved a cycle of correlation largely determined by the competition of organs or parts for a food supply limited in amount or quality. With respect to behavior, the final outcome is a series of telescoped rhythms, which have constituted the objective in this field. The simplest member of this is the daily round of antho-carpotropic movements, which is regularly recurrent and thus passes over into the longer cycles of flower and inflorescence. These lead to the seasonal phenomena that mark the phases of the annual cycle. In annuals this coincides with the life-span; perennials may exhibit a thousand or more floral cycles, while a century plant—probably never a hundred years old—flowers but once and like the annual is monocarpic.

Studies of floral rhythm have been carried on continuously at the Alpine Laboratory as an intrinsic part of the ground-plan for dynamic ecology. The initial endeavors dealt with phenology and floral life-history in the effort to correlate these with measured physical factors at different altitudes. This led directly to experimental attacks upon the opening and closing rhythm or anthokinetics, first by Hensel in 1905 and on a monographic scale by Goldsmith and Hafenrichter in 1932. The round-of-life in connection with experimental pollination was recorded for more than a hundred species, including grasses and composites, by Clements and Long (1923). The transplanting of several hundred species and many thousands of individuals in the climatic transect has furnished cumulative evidence upon the factors that retard or hasten blooming, and especially as to the relative importance of length-of-day. However, the chief opportunity for testing the effectiveness of the latter has been found at Santa Barbara, where the almost frostless winter has yielded novel results to be secured in no other type of climate. The present account of adaptation in rhythm is confined to these, while the data from the region of Pikes Peak will be considered in a later volume.

**Materials and Technique.**—Since the installation of the coastal gardens at Santa Barbara in 1925, some two thousand species have been tested in the various experimental projects. Apart from natives and the tropical and austral exotics favored by the region, these were drawn mainly from the deciduous forest and prairie climaxes, with a con-

siderable number from mountain climates and the desert. The endeavor to establish them and to disclose those best suited to the experimental plan provided data on acclimatization and survival as a by-product, while it contributed directly to the task of correlating floral rhythm with climate. The subclimate of the dune gardens on the seashore, rendered simple the transition to the edaphic series, and these in turn led into the sequences with factor control. Competition cultures afforded another approach to floral behavior, as did likewise a variety of manipulations, such as dividing, excising, cutting-back, injecting, forcing, etc. Age played a part in all such responses, as did season of germination and growth, and in consequence adults and young, seedlings, clones, and underground organs were utilized with a number of specially favorable species.

In order to obtain a norm of reference for adaptive changes in flowering period, recourse was taken to phenological data recorded for a number of years at Lincoln, Nebraska. The generally central location of this region from east to west and north to south and the further advantage as a meeting place of the floras of two great climaxes, prairie and deciduous forest, gave it especial value for this purpose.

#### ADAPTATION IN FLOWERING PERIOD

Ten different types of response have been distinguished, and the species concerned have been arranged in the following tables. The first grouping is into native and garden or ruderal species, and the second by month of blooming. The average time of the opening of the season is indicated by the month, followed by the name of the climax in which the species appears naturally. The general climatic relations may be inferred from this, though some of the species are seral and not climax in character. For exotics, the climax is often not known and hence only the country or region can be given.

For the sake of readers not familiar with the climaxes of North America, the abbreviations are to be explained as follows: Prai, prairie; DFor, deciduous forest; Mon, montane; Bor, boreal; Chap, chaparral; Tund, tundra. Species of wider range in the United States or over the continent are so designated, while those restricted to one or two associations of the prairie bear letters to correspond. Thus, TPr stands for true prairie, MPr for mixed prairie, CPr, coastal prairie, and DPl, desert plains; these may be further shortened when combined, e.g.,

CPDP. The abbreviations for foreign regions are the usual ones, with the possible exception of EuA for Eurasia and Med for the general area about the Mediterranean Sea.

TABLE 1. CHANGE FROM SUMMER TO WINTER BLOOMING

NATIVE			GARDEN OR RUDERAL		
BLOOMING IN DECEMBER					
Species	Normal	Climax	Species	Normal	Source
<i>Achillea alpina</i>	Aug	Tund	<i>Abutilon theophrasti</i>	Aug	India
<i>Adenostoma sparsifolium</i>	Apr	Chap	<i>Alyssum alyssoides</i>	Jul	Eu
<i>Agrimonia striata</i>	Jul	DFor	<i>Anagallis arvensis</i>	Jun	Eu
<i>Anaphalis margaritacea</i>	Aug	Bor	<i>Antirrhinum hispanicum</i>	Jul	Med
<i>Andropogon glomeratus</i>	Sep	DFor	<i>majus</i>	Jun	Med
<i>virginicus</i>	Aug	DFor	<i>Armeria maritima</i>	Jul	Eu
<i>Anemone patens</i>	May	Prai	<i>Avena fatua</i>	Jul	EuA
<i>Aristida purpurea</i>	Jun	Prai	<i>Brassica nigra</i>	Jun	EuA
<i>Aster canescens</i>	Jul	MPr	<i>Bromus catharticus</i>	Jun	SA
<i>ericoides</i>	Sep	DFPr	<i>Calendula officinalis</i>	Jun	SEu
<i>turbinellus</i>	Sep	Prai	<i>Campanula olympica</i>	Jul	Eu
<i>Atriplex canescens</i>	Jul	Prai	<i>pyramidalis</i>	Jun	SEu
<i>Bouteloua chondrosioides</i>	Jul	DPl	<i>rapunculoides</i>	Jul	EuA
<i>curtipendula</i>	Jun	Prai	<i>rapunculus</i>	Jul	Eu
<i>filiformis</i>	Jul	DPl	<i>Catananche coerulea</i>	Jul	SEu
<i>rigidiseta</i>	Jun	CPr	<i>Cheiranthus cheiri</i>	Jun	SEu
<i>trifida</i>	Jun	CPDP	<i>Chenopodium murale</i>	Jun	Eu
<i>Callirhoe involucrata</i>	Jul	Prai	<i>Chrysanthemum coronarium</i>	Jul	SEu
<i>Coreopsis 1.-grandiflora</i>	Jun	DFor	<i>Convolvulus arvensis</i>	Jul	Eu
<i>tinctoria</i>	Jul	Prai	<i>tricolor</i>	Jun	SEu
<i>Dalea formosa</i>	Jul	Prai	<i>Cosmos bipinnatus</i>	Aug	Mex
<i>Delphinium bicolor</i>	Jul	MPr	<i>sulphureus</i>	Aug	Mex
<i>decorum</i>	May	Mon	<i>Cynoglossum pictum</i>	Jul	Eu
<i>Dicentra eximia</i>	Jun	DFor	<i>Delphinium elatum</i>	Jun	Eu
<i>Erigeron canadensis</i>	Jul	NA	<i>Dianthus alpinus</i>	Jul	Eu
<i>ramosus</i>	Jun	TPr	<i>barbatus</i>	Jun	EuA
<i>speciosus</i>	Jul	Mon	<i>carthusianorum</i>	Jul	Eu
<i>Erysimum asperum</i>	Jun	Prai	<i>Gaillardia hybrida</i>	Jun	US
<i>Fallugia paradoxa</i>	Jun	Prai	<i>Geranium pratense</i>	Jun	Eu
<i>Gaillardia aristata</i>	Jul	Prai	<i>Geum urbanum</i>	Jun	Eu
<i>pinnatifida</i>	Jun	Prai	<i>Helianthus annuus</i>	Jul	US
<i>Gaura lindheimeri</i>	Jul	Prai	<i>Heliotropium peruvianum</i>	Jun	Peru
<i>Geum canadense</i>	Jul	DFor	<i>Hypochoeris radicata</i>	Jul	Eu
<i>strictum</i>	Jul	For	<i>Iris pumila</i>	Apr	Eu
<i>Grindelia squarrosa</i>	Sep	Prai	<i>Lactuca virosa</i>	Jul	Eu
<i>Lesquerella argentea</i>	Jun	Prai	<i>Lavandula spica</i>	Jul	Med
<i>Linaria canadensis</i>	Jul	NA	<i>Linaria bipartita</i>	Jun	Med
<i>Lonicera sempervirens</i>	Jun	DFor	<i>vulgaris</i>	Jul	EuA
<i>Malvastrum munroanum</i>	Jul	MPr	<i>Linum austriacum</i>	Jun	Eu
<i>Mertensia alpina</i>	Jul	Tund	<i>Matthiola incana</i>	Jun	SEu
<i>Muhlenbergia emersleyi</i>	Jun	DPl	<i>Medicago sativa</i>	Jul	Eu
<i>Oenothera biennis</i>	Jun	NA	<i>Melilotus alba</i>	Jun	EuA
<i>hookeri</i>	Jul	Prai	<i>Myosotis silvatica</i>	Jun	EuA
<i>lanceolata</i>	Jun	Prai	<i>Oenothera lamarckiana</i>	Jul	Eu
<i>rhombipetala</i>	Jul	MPr	<i>Oxalis corniculata</i>	Jun	Eu
<i>Papaver nudicaule</i>	Jul	Tund	<i>Philadelphus coronarius</i>	May	EuA
<i>Pentstemon arizonicus</i>	Jul	MPr	<i>Poa annua</i>	Jun	EuA
<i>barbatus</i>	Jun	MPr	<i>Primula veris</i>	Jun	Eu
<i>Potentilla gracilis</i>	Jul	Mon	<i>Ranunculus acris</i>	Jun	Eu
<i>Rudbeckia hirta</i>	Jul	US	<i>repens</i>	Jun	Asia
<i>laciniata</i>	Jul	US	<i>Raphanus sativus</i>	Jun	Eu

<i>Sidalcea neomexicana</i>	Jul	MPr	<i>Ruta graveolens</i>	Jul	Eu
<i>Solanum nigrum</i>	Jul	US	<i>Salpinglossis sinuata</i>	Jul	Chile
<i>Solidago canadensis</i>	Aug	NA	<i>Scabiosa atropurpurea</i>	Jul	EuA
<i>humilis</i>	Jul	Mon	<i>Senecio vulgaris</i>	Jun	Eu
<i>h-nana</i>	Aug	Tund	<i>Sonchus oleraceus</i>	Jun	Eu
<i>missouriensis</i>	Aug	TMPPr	<i>Teucrium botrys</i>	Jul	Eu
<i>rigida</i>	Aug	TPr	<i>Trifolium pratense</i>	Jul	Eu
<i>Sporobolus cryptandrus</i>	Jul	Prai	<i>Tropaeolum majus</i>	Jun	SA
<i>Stipa leucotricha</i>	Jun	CPr	<i>Verbascum blatteria</i>	Jul	EuA
<i>pringlei</i>	Jul	DPl	<i>thapsus</i>	Jul	EuA
<i>Thelesperma filifolium</i>	Jul	MPr	<i>Verbena hybrida</i>	Jul	SA
<i>Verbena urticifolia</i>	Aug	DFor	<i>Veronica longifolia</i>	Jun	EuA
<i>Verbesina encelioides</i>	Jul	MPr	<i>Vinca major</i>	Jun	Eu

## BLOOMING IN JANUARY

<i>Asclepias verticillata</i>	Jul	Prai	<i>Bromus commutatus</i>	Jun	Eu
<i>Eragrostis biflora</i>	Jul	DPl	<i>Geum atrosanguineum</i>	Jul	Chile
<i>Geum rivale</i>	Jun	Bor	<i>Stipa capillata</i>	Jul	EuA
<i>Panicum scribnerianum</i>	Jun	TPr	<i>gigantea</i>	Jul	EuA
<i>Potentilla rubricaulis</i>	Jul	Tund	<i>pennata</i>	Jul	EuA
<i>Paspalum leve</i>	Jul	DFor	<i>Verbascum phoeniceum</i>	Jul	EuA

## BLOOMING IN FEBRUARY

<i>Artemisia pattersoni</i>	Aug	Tund	<i>Brassica oleracea</i>	Jul	Eu
<i>Erigeron macranthus</i>	Jul	Mon	<i>Solidago virgaurea</i>	Aug	Eu
<i>Geranium fremonti</i>	Jul	MPr	<i>Tithonia speciosa</i>	Jul	Mex
<i>Pentstemon strictus</i>	Jun	MPr			
<i>Solidago arguta</i>	Aug	DFor			
<i>Stipa comata</i>	Jun	Prai			

The month indicated above for each species marks the beginning of the period of blooming; in most cases it is a general average derived from 8-10 years of observations. However, this does not take into account the wide variation in the opening of the flowering season in Southern California. To plants, this is really a spring that follows a dry summer rather than a cold winter as in temperate climates. The resting period is produced by a lack of rain and a deficit of hoard and not by low temperatures. As a consequence, growth is renewed after the oncoming of adequate rains; this may occur at any time from October to December in response to cosmic events not yet well understood. Late November or early December marks the usual beginning of flowering, but at least half the species listed for the latter may open their blossoms in October when early rains permit. Watering alone brings about this effect only in part, since a drop in seasonal temperature seems to be a secondary requisite. Blossoming was particularly early in 1941, after a summer of moderate temperatures and a previous rainy season of the greatest excess ever recorded.

More than a third of the 400 species under examination for several years displayed their first flowers in December or earlier, though in many, blossoming was interrupted by occasional frosts in January. It



is readily understood that the use of months as units suggests limits that do not exist. However, the falling-off in early January is decisive owing to the cause just given, with the consequence that six times as many species bloom in December as in both the succeeding months.

The range of families and genera and of life-forms represented in the table is so wide as to warrant the conclusion that a displacement of the flowering habit by half-a-year is a common phenomenon. The number of genera is 98, belonging to 28 families distributed from buttercups to mints in one great dicotyl phylum and roses to composites in the other. The monocotyls are represented only by grasses and irids, since most of the forbs available are either spring-bloomers or hydrophytes. The composites supply 21 of the genera, the grasses are next with 8, followed by mustards with 7, roses and figworts with 5, and buttercups, mallows, peas, and borages with 4 each. In short, extreme adaptability in regard to flower rhythm occurs throughout the phyletic lines of seed-plants.

For obvious experimental reasons, the number of woody plants concerned is small, being confined almost wholly to low shrubs that come into bloom after two or three years from seed. Hence, the experimental material consisted predominantly of forbs and grasses, and comprised annuals, biennials and perennials. In the Santa Barbara climate, all of these regularly blossomed the first year from seed though the annuals had the advantage of a shorter vegetative period, and often also of self-sowing to yield out-of-season results. Biennials maintained the usual rosette habit, but in default of winter exhibited no interruption of the growth rhythm as a rule. Many of the annuals developed either an evergreen or woody habit to become short-lived perennials and in some degree, ever-bloomers. The flowering habits of a considerable number of perennials were also modified by a persistent rosette or cluster of evergreen leaves, as well as by the development of woody stems (Plates 35-37).

With respect to climate, the native species were drawn from six different climaxes, but with the several associations of the prairie contributing more than half. Species from the deciduous forest were second in number and agreed with those from the prairie in the time of normal maximum and in adjusted response. In most cases, the seeds were obtained from the cold temperate half of the two climaxes and some had been grown in gardens for a time. Taken together with the amount of fluctuation possible from season to season, these may serve

to explain the lack of difference in behavior and the absence of any evident fixity of habit. Some of the grasses, such as *Bouteloua*, show definite climatic strains as to growth and flowering, and the forbs doubtless behave in like fashion. While flowering time can be strikingly displaced in most of these, the strains of each species tend to maintain their relative positions. The reciprocal transplanting of alpine and plains species in the Pikes Peak transect furnishes the most graphic instances of such phenomena, as is indicated later.

Cultivated and ruderal species from abroad have so long been subjected to the artificial edaphic conditions of gardens and other disturbed places that their response to new habitats is even more rapid and complete than that of natives.

TABLE 2. CHANGE FROM SUMMER TO SPRING BLOOMING

## BLOOMING IN MARCH

Species	Normal	Climax	Species	Normal	Climax
<i>Agropyrum dasystachyum</i>	Jul	Pai	<i>Pentstemon albidus</i>	Jun	Prai
<i>Anemone canadensis</i>	Jun	Prai	<i>Ranunculus acris</i>	Jul	DFPr
<i>multifida</i>	Jul	Bor	<i>Schizachne purpurascens</i>	Jul	Mon
<i>Aquilegia chrysantha</i>	Jul	Mon	<i>Stipa neomexicana</i>	Jun	MPr
<i>coerulea</i>	Jul	Mon	<i>spartea</i>	Jun	TPr
<i>Buchloe dactyloides</i>	Jul	Prai	<i>williamsi</i>	Jul	Pai
<i>Cowania stansburiana</i>	Jul	DPl	<i>Viola canadensis</i>	Jun	DFor
<i>Delphinium azureum</i>	Jun	Prai			
<i>Erigeron uniflorus</i>	Jul	Tund			
<i>Gentiana frigida</i>	Aug	Tund			
<i>Koeleria cristata</i>	Jun	Prai			
<i>Linum perenne</i>	Jun	Prai			
<i>Mirabilis multiflora</i>	Jul	MPr			
<i>Muhlenbergia emersleyi</i>	Jun	DPl			
<i>montana</i>	Jul	MPr			
<i>Oenothera drummondii</i>	Jun	CPr			
<i>missouriensis</i>	Jul	Prai			

## GARDEN OR RUDERAL

<i>Anchusa italica</i>	Jul	Med
<i>Aquilegia alpina</i>	Sum	EuA
<i>sibirica</i>	Sum	Sib
<i>Brassica campestris</i>	Sum	Eu
<i>Cynoglossum amabile</i>	Jul	Eu
<i>Festuca elatior</i>	Jul	Eu

## BLOOMING IN APRIL

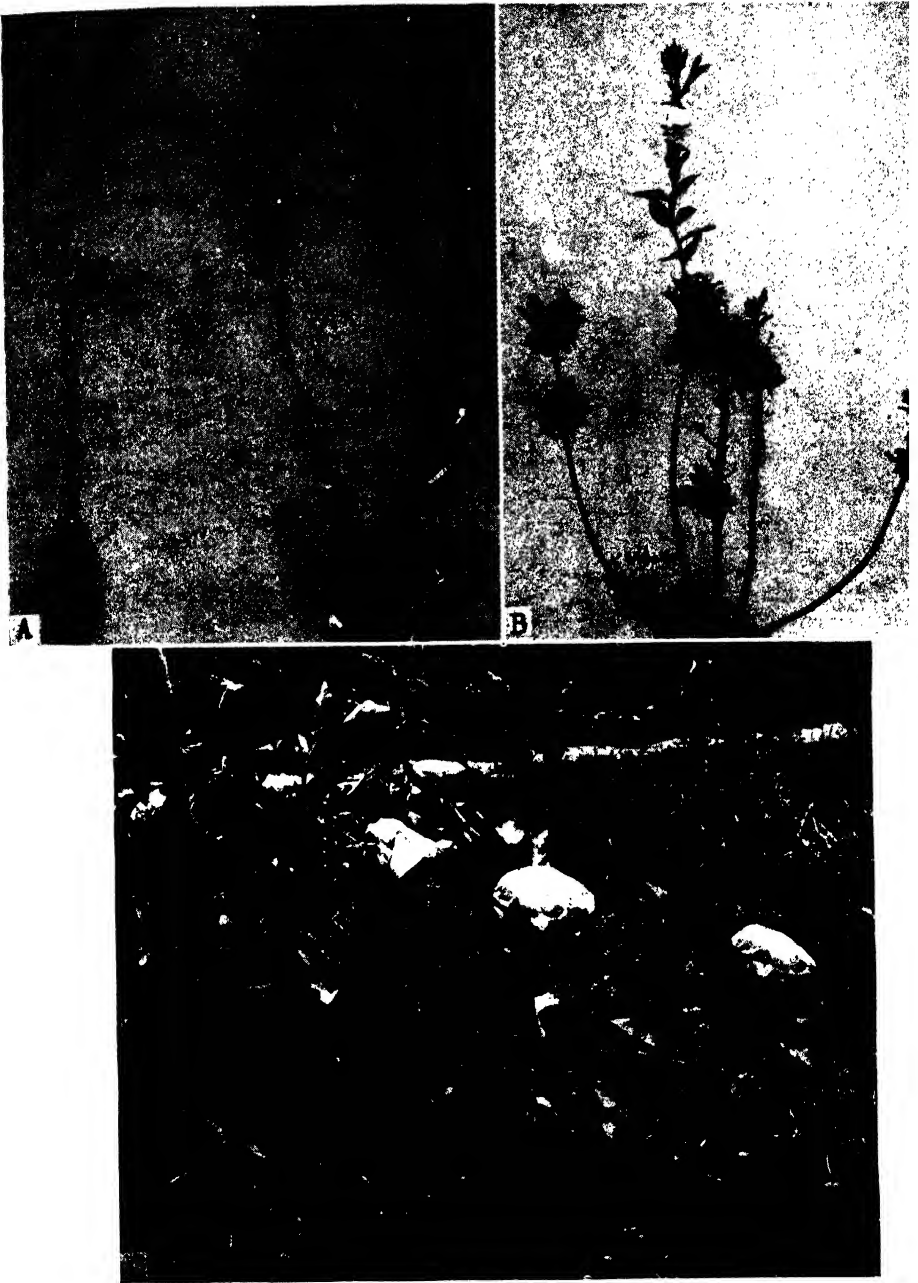
<i>Agrostis hiemalis</i>	Jul	PrMon	<i>Festuca ovina</i>	Jul	Prai
<i>Andropogon scoparius</i>	Aug	DFPr	<i>rubra</i>	Jul	Prai
<i>Aster azureus</i>	Sep	DFor	<i>Gymnolomia multiflora</i>	Aug	PrMon
<i>cordifolius</i>	Sep	DFor	<i>Manisuris cylindrica</i>	Aug	DFCPr
<i>levis</i>	Sep	DFPr	<i>Penstemon glaber</i>	Jul	Mon
<i>novi-belgi</i>	Sep	DFor	<i>unilateralis</i>	Jun	Prai
<i>Campanula rotundifolia</i>	Jul	US:NA	<i>Scrophularia nodosa</i>	Jul	DFor
<i>Euphorbia corollata</i>	Aug	DFPr	<i>Triodia albescens</i>	Jul	DFPr
<i>Delphinium scopulorum</i>	Jul	PrMon	<i>pilosa</i>	Jul	DPl

## BLOOMING IN MAY

<i>Campanula alpina</i>	Aug	Tund	<i>Ruellia ciliosa</i>	Aug	DFPr
<i>Helianthus maximiliani</i>	Sep	Prai	<i>Sporobolus cryptandrus</i>	Aug	Prai
<i>Liatis squarrosa</i>	Aug	Prai	<i>Verbena stricta</i>	Aug	DFPr
<i>Paspalum stramineum</i>	Aug	Prai			



Change in Life-form of *Oenothera tricocalyx*; Dune Shelter Garden.  
A. Bush form on higher slope.  
B. Normal form in hollow, with plants dwarfed along drier edge.



Changes in Blooming and Life-form.

A. *Verbesina encelioides*, re-blooming in December.

B. *Oenothera hookeri*; shrub-form.

C. *Datura meteloides*: shrub-form with old stems marked by a white tag at base.

PLATE 37



Changes in Blooming and Life-form.

- A. *Psilostrophe cooperi*: Earliest blooming next to warm sand.  
 B. *Gaillardia aristata*: 1. Normal head; 2. Late-season head.  
 C. *Gaillardia hybrida*: Dune Garden forms: 1. Normal; 2. Bush-form.

With respect to change of rhythm, this group differs from the preceding chiefly in being three rather than six months earlier on the average. No plausible reason for this can be seen in the climatic relations, at least in the case of the plants flowering in March, since both months and climaxes are much the same. However, nearly half the species for April blossom in August or September and all of those for May, suggesting that these are marked by a slower rate of development. This leads to their growth being halted by frosty nights; normally this can again be set in motion only by the warm days of late February or early March. The view that garden plants adjust themselves more readily than natives appears to be supported by the small number of aliens.

TABLE 3. FLOWERS OF SPRING OR EARLY SUMMER, OPENING  
ONE-TWO MONTHS IN ADVANCE

BLOOMING IN FEBRUARY

Species	Normal	Climax	Species	Normal	Climax
<i>Caltha palustris</i>	Apr	DFPr	<i>Hepatica triloba</i>	Apr	DFor
<i>Cercis canadensis</i>	Apr	DFor	<i>Mertensia virginica</i>	Apr	DFor
<i>Chamaedaphne calyculata</i>	Apr	Bor	<i>Pieris floribunda</i>	May	Bor
<i>Claytonia virginica</i>	Apr	DFor	<i>Viola cucullata</i>	Apr	DFor

BLOOMING IN MARCH

<i>Aquilegia canadensis</i>	May	DFor	<i>Oxalis violacea</i>	May	DFPr
<i>Arisaema triphyllum</i>	May	DFor	<i>Sanguinaria canadensis</i>	Apr	DFor
<i>Baptisia leucophaea</i>	May	TPr	<i>Thalictrum dioecum</i>	May	DFor
<i>Epigaea repens</i>	Apr	Bor	<i>Thalictrum polygamum</i>	May	DFor
<i>Erythronium americanum</i>	Apr	DFor	<i>Tradescantia virginiana</i>	May	DFPr
<i>Geranium maculatum</i>	May	DFor	<i>Trillium cernuum</i>	Apr	DFor
<i>Kalmia latifolia</i>	May	Bor	<i>Trillium erectum</i>	Apr	DFor
<i>Leucothoe catesbaei</i>	Apr	Bor	<i>Trillium grandiflorum</i>	May	DFor
<i>Lithospermum linearifolium</i>	May	Prai			

BLOOMING IN APRIL

Species	Normal	Climax	Species	Normal	Climax
<i>Amorpha fruticosa</i>	May	US	<i>Iris versicolor</i>	May	DFor
<i>Asarum canadense</i>	May	DFor	<i>Orchis spectabilis</i>	May	DFor
<i>Astragalus crassicaulus</i>	Apr	Prai	<i>Pentstemon cobaea</i>	May	TPr
<i>Baptisia tinctoria</i>	Jun	DFor	<i>Pentstemon grandiflorus</i>	May	TPr
<i>Clintonia umbellulata</i>	May	DFor	<i>Salvia farinacea</i>	May	CPr
<i>Cypripedium acaule</i>	May	Bor	<i>Scutellaria resinosa</i>	Jun	MPr
<i>Cypripedium reginae</i>	May	Bor	<i>Stanleya pinnata</i>	Jun	MPr
<i>Disporum lanuginosum</i>	May	DFor	<i>Uvularia grandiflora</i>	May	DFor
<i>Dodecatheon meadia</i>	May	DFPr	<i>Uvularia perfoliata</i>	May	DFor
<i>Gaura lindheimeri</i>	Jun	Prai	<i>Uvularia sessilifolia</i>	May	DFor
<i>Halesia carolina</i>	Apr	DFor	<i>Viola pedata</i>	May	DFPr
<i>Hilaria jamesi</i>	Jun	MPr	<i>Viola sagittata</i>	May	DFor
<i>Hypoxis hirsuta</i>	May	DFor			
<i>Iris missouriensis</i>	May	Prai			

## BLOOMING IN MAY

<i>Agropyrum caninum</i>	Jul	Eu	<i>Malvastrum munroanum</i>	Jul	MPr
<i>Andropogon ischaemum</i>	Jul	Eu	<i>Pentstemon angustifolius</i>	Jun	MPr
<i>Argemone hispida</i>	Jul	MPr	<i>cristatus</i>	Jun	MPr
<i>Arenatherum elatius</i>	Jun	Eu	<i>Petalostemon candidus</i>	Jun	TMPr
<i>Bouteloua eriopoda</i>	Jul	DPl	<i>purpureus</i>	Jun	TMPr
<i>gracilis</i>	Jul	MPr	<i>Polygonatum commutatum</i>	May	DFor
<i>hirsuta</i>	Jul	MPr	<i>Potentilla arguta</i>	Jun	TPr
<i>Bromus inermis</i>	Jul	Eu	<i>Psoralea floribunda</i>	Jun	TMPr
<i>Echinacea pallida</i>	May	TPr	<i>Scutellaria galericulata</i>	Jul	DFor
<i>Habenaria psycodes</i>	Jul	Bor	<i>Smilacina racemosa</i>	Jun	DFor
<i>Heliopsis helianthoides</i>	Jul	DFor	<i>Stipa viridula</i>	Jul	MPr
<i>Lilium canadense</i>	Jun	DFor	<i>Yucca glauca</i>	May	TMPr

## BLOOMING IN JUNE

<i>Echinacea angustifolia</i>	Jun	TMPr	<i>Rudbeckia amplexicaulis</i>	Jun	DFPr
<i>purpurea</i>	Jul	DFor	<i>Sidalcea neomexicana</i>	Jul	MPr
<i>Muhlenbergia torreyi</i>	Jul	MPr	<i>Sporobolus wrightii</i>	Jul	Prai

In general, the species flowering in February and March anticipated their normal period by two months, while in the remaining three groups an advance of a month was the rule. This behavior is probably to be referred to the fact that the majority occur in shady habitats, chiefly deciduous forest. These number 48 out of the total of 77, with ratios of 23 to 25 for February-March, 17 to 26 for April, and only 8 to 26 for May and June. Moreover, most of the shade species are geophytes with relatively large stores of food that explain their early blooming. For the first three months, more than a third of the species belong to this life-form typical of woodland; for the last two, the number is barely a tenth of the total.

Of the 49 species in the following table, 34 blossomed one month earlier at Santa Barbara than in their proper climaxes, while for 15 of them flowering occurred in the same month, usually July. The difference of a month was not a mere fluctuation but a regular event, though an occasional early date causes a few species to appear also in one or the other of the preceding tables. The deciduous forest climax, with or without the prairie, comprised 35 of the total and the prairie alone but 13, largely of southern origin. However, the number of shade species is small, reaching a mere half-dozen.

TABLE 4. STABLE SUMMER BLOOMERS, MOSTLY A MONTH OR LESS EARLIER

Month	Species	Normal	Climax	Month	Species	Normal	Climax
Jul	<i>Agastache anethiodora</i>	Jul	TMPr	Aug	<i>Helianthus rigidus</i>	Aug	Prai
Jul	<i>nepetoides</i>	Jul	DFor	Jun	<i>Hibiscus trionum</i>	Aug	DFPr
Jul	<i>Allium stellatum</i>	Jul	TMPr	Jun	<i>Lepachys pinnata</i>	Jul	DFor
Jul	<i>Andropogon halli</i>	Aug	Prai	Jul	<i>Liatris scariosa</i>	Aug	DFPr
Jul	<i>furcatus</i>	Aug	DFPr	Jul	<i>spicata</i>	Aug	DFor
Jul	<i>ternarius</i>	Sep	DFPr	Jul	<i>Lobelia cardinalis</i>	Aug	DFPr
Jul	<i>Asclepias incarnata</i>	Jul	DFPr	Jun	<i>Monarda fistulosa</i>	Jul	DFPr
Aug	<i>Aster cordifolius</i>	Sep	DFor	Jul	<i>pectinata</i>	Jul	Prai
Jul	<i>macrophyllus</i>	Aug	DFor	Jul	<i>punctata</i>	Jul	DFPr
Jul	<i>multiflorus</i>	Aug	Prai	Jul	<i>Panicum virgatum</i>	Aug	DFPr
Aug	<i>novae-angliae</i>	Sep	DFPr	Jun	<i>Redfieldia flexuosa</i>	Jul	Prai
Jul	<i>Calamovilfa gigantea</i>	Jul	Prai	Jun	<i>Scrophularia marylandica</i>	Jul	DFor
Jul	<i>Cassia fasciculata</i>	Jul	DFPr	Jul	<i>Silphium integrifolium</i>	Aug	DFPr
Jun	<i>Cleome lutea</i>	Jul	Prai	Jul	<i>laciniatum</i>	Aug	DFPr
Jun	<i>serrulata</i>	Jul	Prai	Jun	<i>perfoliatum</i>	Jul	DFor
Jun	<i>Datura stramonium</i>	Jul	DFPr	Jul	<i>terebinthinaceum</i>	Aug	DFPr
Jul	<i>Dracopcephalum virginianum</i>	Jul	DFor	Jul	<i>Solidago rigida</i>	Aug	DFPr
Aug	<i>Eupatorium coelestinum</i>	Aug	DFor	Jul	<i>sempervirens</i>	Aug	DFor
Aug	<i>purpureum</i>	Aug	DFor	Jul	<i>serotina</i>	Aug	DFPr
Aug	<i>Haplopappus ciliatus</i>	Aug	Prai	Jul	<i>speciosa</i>	Aug	DFPr
Jul	<i>Helenium autumnale</i>	Aug	DFPr	Jun	<i>Verbena hastata</i>	Jul	DFPr
Jul	<i>Helianthella quinquefolia</i>	Aug	Mon	Jun	<i>stricta</i>	Jul	DFPr
Aug	<i>Helianthus giganteus</i>	Sep	DFPr	Jul	<i>Vernonia baldwini</i>	Aug	Prai
Aug	<i>mollis</i>	Aug	DFPr	Jul	<i>noveboracensis</i>	Aug	DFor
Sep	<i>orgyalis</i>	Sep	Prai				

Of greater importance is the fact that 37 of the 49 plants belong to the relatively late-flowering gamopetalous families, with 26 of them composites. More significant still is their post-seasonal behavior, which is quite unlike that of the species previously considered. With practically no exceptions at Santa Barbara, the stems die back and break off, leaving the rootstock hidden in the ground; the few annuals die completely of course. Furthermore, the perennials are mostly robust and the composites in particular are tall, some as much as ten to twelve feet, so that a long season is required for their full development. This is equivalent to saying that they require the greatest number of heat units of all the plants treated experimentally. The shoots do not appear until March and about the time fogs begin, with the consequence that the acceleration generally typical of the climate is much reduced or entirely absent. This conclusion is further supported by the response of species grown in both sun and shade; the latter flowered about two months later owing to reduced radiation.



TABLE 5. REPEATS AND EVER-BLOOMERS

Species	Climax	Species	Climax
<i>Achillea alpina</i>	Tund	<i>Helianthus annuus</i>	Rud
<i>millefolium</i>	US	<i>Hypochoeris radicata</i>	Rud
<i>Adenostoma sparsifolium</i>	Chap	<i>Iris pumila</i>	Cult
<i>Agrimonia striata</i>	DFor	<i>Isomeris arborea</i>	CSb
<i>Agrostis verticillata</i>	Rud	<i>Lavandula spica</i>	Cult
<i>Alyssum maritimum</i>	Cult	<i>Lepachys columnaris</i>	TMPr
<i>Anaphalis margaritacea</i>	Mon	<i>Lesquerella argentea</i>	Prai
<i>Andropogon glomeratus</i>	DFor	<i>Leucothoe catesbaei</i>	Bor
<i>virginicus</i>	DFor	<i>Linaria bipartita</i>	Cult
<i>Anemone patens</i>	Prai	<i>vulgaris</i>	Rud
<i>Antirrhinum hispanicum</i>	Cult	<i>Lonicera sempervirens</i>	DFor
<i>speciosum</i>	Chap	<i>Matthiola incana</i>	Cult
<i>Arctotis grandis</i>	Cult	<i>Medicago sativa</i>	Cult
<i>Armeria alpina</i>	Cult	<i>Melica californica</i>	CalPr
<i>maritima</i>	Cult	<i>Melilotus alba</i>	Cult
<i>Asclepias galioides</i>	MPr	<i>Mimulus aurantiacus</i>	CSb
<i>subulata</i>	Des	<i>Muhlenbergia emersleyi</i>	DPl
<i>Aster canescens</i>	MPr	<i>Nicotiana glauca</i>	Rud
<i>spinosus</i>	Des	<i>tabacum</i>	Cult
<i>turbinellus</i>	Prai	<i>Oenothera biennis</i>	Rud
<i>Avena fatua</i>	Rud	<i>b-lanceolata</i>	Rud
<i>Baileya multiradiata</i>	Des	<i>hookeri</i>	Cal
<i>Bignonia cherere</i>	Cult	<i>lamarckiana</i>	Cult
<i>stans</i>	Cult	<i>rhombipetala</i>	MPr
<i>venusta</i>	Cult	<i>Oryzopsis miliacea</i>	Cult
<i>Bouteloua curtipendula</i>	Prai	<i>Oxalis corniculata</i>	Rud
<i>Bromus catharticus</i>	Rud	<i>bowei</i>	Cult
<i>commutatus</i>	Rud	<i>Panicum scribnerianum</i>	TPr
<i>Callirhoe involucrata</i>	Prai	<i>Paspalum dilatatum</i>	Cult
<i>Campanula rapunculoides</i>	Cult	<i>Pentstemon antirrhinoides</i>	CSb
<i>Chrysanthemum coronarium</i>	Cult	<i>barbatus</i>	Mon
<i>Commelina coelestis</i>	Cult	<i>gloxinioides</i>	Cult
<i>Coreopsis l.-grandiflora</i>	DFor	<i>heterophyllus</i>	Cult
<i>tinctoria</i>	Prai	<i>palmeri</i>	Prai
<i>Dalea formosa</i>	Prai	<i>parishi</i>	CalPr
<i>Datura meteloides</i>	Des	<i>spectabilis</i>	Chap
<i>Delphinium bicolor</i>	MPr	<i>Petunia hybrida</i>	Cult
<i>elatum</i>	Cult	<i>Psilostrophe cooperi</i>	Des
<i>Encelia actoni</i>	Des	<i>Rosmarinus officinalis</i>	Cult
<i>californica</i>	CSb	<i>Rudbeckia hirta</i>	US
<i>farinosa</i>	Des	<i>Ruta graveolens</i>	Cult
<i>frutescens</i>	Des	<i>Salpinglossis sinuata</i>	Cult
<i>media</i>	Cult	<i>Salvia farinacea</i>	CPr
<i>Eragrostis curvula</i>	Cult	<i>greggi</i>	CPr
<i>intermedia</i>	DPl	<i>Saponaria officinalis</i>	Rud
<i>lugens</i>	DPl	<i>Senecio salignus</i>	DPl
<i>Erigeron canadensis</i>	Rud	<i>Solanum douglasii</i>	CalPr
<i>glaucus</i>	CalPr	<i>sanitwongsi</i>	Cult
<i>macranthus</i>	Cult	<i>wallacei</i>	CalPr
<i>ramosus</i>	TPr	<i>xanti</i>	CalPr
<i>Eschscholtzia californica</i>	Cult	<i>Solidago arguta</i>	DFor
<i>Gaillardia hybrida</i>	Cult	<i>canadensis</i>	DFor
<i>Gaura lindheimeri</i>	Prai	<i>humilis</i>	Mon
<i>Geranium pratense</i>	Cult	<i>missouriensis</i>	TMPr
<i>Geum rivale</i>	Mon	<i>rigida</i>	TPr
<i>strictum</i>	Mon	<i>virguarea</i>	Bor
<i>urbanum</i>	Cult	<i>Sonchus oleraceus</i>	Rud
<i>Godetia fremonti</i>	Cult	<i>Sporobolus poireti</i>	Rud
<i>Grindelia blakei</i>	CalPr	<i>Statice limonium</i>	Cult

Species	Climax	Species	Climax
<i>Stanleya pinnata</i>	Prai	<i>Trichostema lanatum</i>	Chap
<i>Stipa hyalina</i>	SA	<i>Trifolium pratense</i>	Cult
<i>leucotricha</i>	CPr	<i>Triodia congesta</i>	Prai
<i>papposa</i>	SA	<i>Trixis californica</i>	Des
<i>pringlei</i>	DPI	<i>Tropaeolum majus</i>	Cult
<i>pulchra</i>	CalPr	<i>Verbascum blattaria</i>	Rud
<i>Strelitzia reginae</i>	Cult	<i>thapsus</i>	Rud
<i>Tecomaria capensis</i>	Cult	<i>Verbena erinoides</i>	Cult
<i>Teucrium botrys</i>	Cult	<i>urticifolia</i>	DFor
<i>Tinantia erecta</i>	Cult	<i>Verbesina encelioides</i>	Prai
<i>Tithonia speciosa</i>	Cult	<i>Veronica spicata</i>	Cult

The greater uniformity of a subtropical climate by comparison with a temperate or boreal one is necessarily reflected in floral behavior. With smaller differences in temperature between seasons and especially with irrigation during the dry summer, continued recurrent blossoming becomes a common phenomenon. In the most equable situations, such as southerly slopes along the foothills, frost may be entirely absent and growth and flowering may occur at almost any time or continue indefinitely. This is peculiarly the situation at Santa Barbara, where the chain of islands, the southern aspect, mid-season fog, and the rim of mountains combine to produce a unique local climate. Even in the experimental garden in Mission Canyon with a cold-air stream at night, some winters pass without a trace of frost and material damage from it is all but unknown. Hence, growth is seldom interrupted by reason of low temperatures, though it may be slowed down during January and February in the cooler winters. By contrast, it ceases more or less regularly and completely in the rainless summer, except where moisture is still available in the soil. This is naturally the case in gardens, so that plants flower that have not done so earlier and those that have may bloom again.

The general rule is that the colder nights of midwinter delay or interrupt blossoming and that a similar effect is produced by hot dry periods in the summer. Moreover, the stage of development already attained plays a large and often decisive part in the rhythmic response. For example, plants that have provided an adequate photosynthetic equipment by January are slowed down but little and bloom correspondingly earlier, which is true of both species and individuals. On the other hand, those still in the seedling stage may mark time for a month or two, with a corresponding delay in flowering. A unique instance of such a standstill was afforded by *Leucothoe catesbaei*, growing under a canopy of live-oaks. The lowermost flower or two of each raceme had opened in late December just before the advent of frosty

nights; under the protection of the trees these remained fresh until blooming was resumed toward the end of March.

The 110 species of the list comprise those studied throughout the period of ten years, though as many more are represented by occasional records. With respect to climax or source, it is noteworthy that species from the deciduous forest, which are mostly cold-temperate in nature, are few, being outnumbered by those from the subtropical regions, desert, California prairie and sagebrush. The range of families and genera is sufficiently great to suggest that recurrent blooming is to be expected in most species grown in frost-free climates. The reason for the large number of cultivated forms is probably to be found in their many generations under equable conditions, and some confirmation of this has been secured with particular species. As an illustration of this response, *Erigeron macranthus* grown for a generation in the flower garden from cultivated seed is an ever-bloomer for nine months or more of the year, while plants from seed collected in its native habitat at the Alpine Laboratory flower for but two or three months in early summer and only a month before their normal period.

Another type of recurrence is exhibited by a considerable number of annuals and biennials that undergo a change of life-form to become short-lived woody perennials or soft-wood shrubs. Common examples are furnished by species of *Oenothera*, sections *Anogra* and *Onagra*, and of *Verbascum*. In these, green branches from the old stems flower in autumn and winter, while new herbaceous shoots are developing from the basal rosettes. (Plates 35B, 36B).

The great majority of the native species of southern California flower in winter or early spring, and this is true likewise of a large number of tropical and austral exotics. In years with late rains, flowering may continue into June, but below the mountains few species come into blossom after the first of May. It has already been noted that the opening of the growing season may vary two or three months, from late September to December, in response to the incidence of good rains, and similar fluctuations occur in Spring. This is true not merely of the close of the season, but it may be even more striking in the case of the maximum. This is naturally most pronounced in the wetter years, when adequate holarid continues through the rising temperatures about the equinox. Such a conjunction varies a month or two in time, and such years with their amazing flush of bloom afford a vivid contrast to the amount and timing of bloom during dry seasons.

Since annuals undergo the maximum displacement in rhythm, these have been chiefly employed in the investigation of this. Graduated series of direct factors have been employed in connection with adaptation in growth and form, as discussed later, and changes in time of seeding and planting have been used to produce greater shifts. In addition, species with the summer habit have been transferred from the Alpine Laboratory to Santa Barbara and then moved back to Pikes Peak after a few years. Furthermore, seedlings of selfed populations have been grown under warmer and cooler conditions to hasten and retard the time of blooming.

Somewhat more than 50 species of annuals were concerned in these experiments, mostly natives together with a few cultivated ones. The universal rule was to the effect that time of blooming was closely correlated with date of sowing and that this was modified in some degree by the character of the season, especially the number of frosts when these occurred. Plants in the greenhouse flowered four to six weeks before those in the gardens, and the latter preceded those in nature by much the same interval when rains were deficient. The reduction of light intensity to about 20 percent sometimes delayed blossoming as long as two months, while the retarding influence of wet soil was about half of this.

The greatest effect was naturally felt by the California annuals grown at the Alpine Laboratory where the maximum displacement was five to six months at the Plains and Montane Gardens and a month or so more at the Alpine Garden. These were sown in the early spring at the Plains Garden and distributed to the other two when the season was sufficiently advanced to avoid frost. At first, a few were grown in California and the seedlings shipped to Colorado by aeroplane, but it was found that such an early start was not necessary. A smaller number of perennials blooming at different times from December to April postponed opening their flowers until the latter half of the summer. Montane species sent to Santa Barbara adjusted themselves to the earlier seasons there, and reverted to their original habits when brought back to Pikes Peak. Alpine transfers were uniformly very early, often flowering at Santa Barbara in December and January.

With the object of testing the universal nature of change of flowering rhythm, attention has been turned to the Antipodes. Australian species to the number of a hundred or more have been brought into gardens at Santa Barbara, and in return more than twice that number

of immigrants have reached Australia from the northern hemisphere, mostly ruderals and gardens escapes. Equally fortunate is the fact that Ewart in his "Flora of Victoria" has gone far beyond the usual practice of botanists in his complete and painstaking account of the opening and duration of flowering. As a consequence, it becomes possible to make a reciprocal comparison between the two hemispheres on the basis of exotics grown at Santa Barbara and of ruderals and cultivated species found generally throughout the United States.

This examination reveals that the great majority of species in both groups reverse the calendar, just as do the seasons. The common period of blooming in austral regions is from September to March, with the optimum from December to February. Practically all the ruderals and garden plants from the northern hemisphere fall in this period of the southern summer. The displacement is less complete with most of the exotics brought to California because of a barrier of a rainless summer. Moreover, the majority of these are trees that are somewhat less dependent upon the march of the seasons. *Eucalyptus* in particular is highly irregular in rhythm in its homeland, but loses much of this flexibility in California, where blooming is regularly in the springtime. *Acacia*, on the other hand is much more uniform, beginning to blossom in August or September in Australia and preferring February at Santa Barbara. As a result, the control of the flowering rhythm by climatic conditions is all but complete and confirms on a large scale the experimental response discussed in preceding pages.

#### RHYTHM IN FACTOR GRADIENTS

The modification of flowering rhythm exhibited on a large scale by transfers from one climate to another is to be seen in lesser degree in the several adaptation series under partial control. This reduced effect is in accord with the fact that the differences in each gradient are relatively small and necessarily operate under the general control of the local climate. The dates of flowering tabulated here are for nutrients, light, soils, and length-of-day; similar though less uniform results were obtained at the dune gardens, for in-and-out sheds, and for competition cultures.

TABLE 6. DATES OF BLOOMING IN THE NUTRIENT-WATER SERIES

SPECIES	NW-2	NW-1	NW-0
<i>Achillea alpina</i> - - - -	4/11	4/13	4/15
<i>Agoseris heterophylla</i> - - - -	5/ 4	5/ 7	5/12
<i>Agrostemma githago</i> - - - -	5/13	5/11	5/10
	5/10	5/ 8	5/ 5
	5/11	5/11	5/11
<i>Anagallis linifolia</i> - - - -	5/ 3	5/ 7	5/10
<i>Antirrhinum hispanicum</i> - - - -	5/ 4	5/ 7	5/ 8
	5/ 5	5/ 8	5/18
<i>Aquilegia truncata</i> - - - -	5/ 8	5/ 9	5/12
<i>Callirhoe involucrata</i> - - - -	4/28	4/30	5/11
<i>Chrysanthemum coronarium</i> - - - -	4/ 3	4/ 3	4/ 8
<i>Clarkia elegans</i> - - - -	4/15	4/15	4/15
<i>Collinsia bicolor</i> - - - -	3/30	4/ 3	4/ 9
<i>Coreopsis 1-grandiflora</i> - - - -	5/ 1	5/ 6	5/12
<i>tinctoria</i> - - - -	5/ 6	5/ 8	5/12
<i>Cosmos bipinnatus</i> - - - -	2/19	3/ 1	3/ 3
<i>sulphureus</i> - - - -	3/24	4/ 1	4/20
<i>Cynoglossum amabile</i> - - - -	4/16	4/20	4/30
<i>Geum atrosanguineum</i> - - - -	4/21	4/17	4/26
<i>strictum</i> - - - -	5/ 7	5/10	5/12
<i>Gilia tricolor</i> - - - -	2/23	2/21	2/25
<i>Godetia amoena</i> - - - -	5/ 1	5/ 6	5/12
<i>dudleyana</i> - - - -	4/ 9	4/ 9	4/15
<i>grandiflora</i> - - - -	4/27	5/10	5/12
	4/ 5	4/12	4/17
<i>Linum lewisi</i> - - - -	4/10	4/18	4/18
	4/ 9	4/15	4/20
<i>Mimulus cardinalis</i> - - - -	5/19	5/26	5/31
<i>Madia elegans</i> - - - -	4/ 3	4/ 5	4/13
<i>Oenothera trichocalyx</i> - - - -	4/18	4/20	4/23
<i>Pentstemon barbatus</i> - - - -	5/ 4	5/ 8	5/12
<i>Phacelia grandiflora</i> - - - -	1/28	2/ 1	1/30
<i>Raphanus sativus</i> - - - -	1/24	1/26	1/25
<i>Rudbeckia amplexicaulis</i> - - - -	5/27	5/30	5/31
<i>Sisyrinchium angustifolium</i> - - - -	5/18	5/20	5/20
<i>Solanum douglasi</i> - - - -	4/23	4/25	5/10
<i>Stipa pulchra</i> - - - -	3/ 9	3/18	3/22
<i>Verbena prostrata</i> - - - -	5/ 3	5/ 4	5/ 9
<i>Verbesina encelioides</i> - - - -	3/12	3/ 9	3/18
<i>Viola tricolor</i> - - - -	3/14	3/19	3/28

Of the 40 entries in the table, 28 progress regularly from plot NW-2 with optimum amounts of fertilizer and water to NW-0 with nothing added. Three species flowered in the reverse order and in five NW-1 was the earliest. The time interval between plots was much less uniform, since a few exceptionally warm, cold or wet days exerted a decisive effect in hastening or retarding the first flowers. Two species, *Agrostemma githago* and *Clarkia elegans*, blossomed on the same day in all three plots; for the two years preceding, the latter reversed the usual sequence. In half the cases, the interval between the first and third plots was approximately two weeks, with a period of four in *Cosmos sulphureus*.

TABLE 7. DATES OF BLOOMING IN THE LATH-HOUSE SERIES

SPECIES	60% LH-1	35% LH-2	20% LH-3	10% LH-4	5% LH-5
<i>Agrostemma githago</i> - - -	5/10	5/11	5/15	5/20	5/27
	5/11	5/20	5/22	5/25	
<i>Antirrhinum hispanicum</i> - -	5/ 8	5/20	6/ 1		
<i>Chrysanthemum coronarium</i> -	3/26	4/15	4/22	5/10	5/29
<i>Clarkia elegans</i> - - - -	4/18	5/ 1	5/ 5	5/10	5/10
<i>rhomboidea</i> - - - -	4/20	4/22	4/22	5/ 8	
<i>Collinsia bicolor</i> - - - -	4/ 8	4/10	4/20	5/ 1	5/ 5
<i>Cosmos bipinnatus</i> - - - -	3/ 7	3/20	3/24	4/ 5	
<i>Cynoglossum amabile</i> - - -	5/10	5/11	5/13		
<i>Godetia grandiflora</i> - - -	4/12	4/16	5/ 6		
<i>Linum lewisii</i> - - - -	5/ 5	5/10	5/13		
<i>Madia elegans</i> - - - -	4/15	4/18	5/10	5/13	
<i>Oenothera trichocalyx</i> - - -	4/27	4/29	5/13		
<i>Raphanus sativus</i> - - - -	3/28	4/ 5	4/15		
<i>Rudbeckia amplexicaulis</i> - -	5/30	6/ 4	6/10		
<i>Stipa leucotricha</i> - - - -	2/25	4/15	4/25	5/15	5/31
<i>Viola tricolor</i> - - - -	3/30	4/ 1	4/ 8	5/13	

With almost no exceptions, the order of flowering in the five lath-houses was from number 1, which received the most radiation to number 5 with the least. The respective percentages were 60, 35, 20, 10, and 5. The intervals were much longer as a rule than for the series in sunlight, owing to the deficit of both light and heat. This was not sufficient in LH-1 to produce a definite difference, so that flowers opened here at about the same time as in the sun. What was lost in terms of food production was compensated for by higher temperatures at night and on cold windy days, though this varied considerably with the character of the season. For example, during one year the ratio of dry weights for sun and the two brightest lath-houses was 9:7:4, while the next year it was 11:4:1.5. Similarly, plants in lath-houses 4 and 5 bloomed only during the warmer drier seasons. In spite of a removable canvas cover, to prevent soil saturation, the aeration of the soil was often defective for periods of several weeks, so that slugs and cut-worms were most injurious likewise. The final consequence was the practical elimination of all species and individuals in these two houses by the end of the growing season. Their low vitality is indicated by the final dry weights, which on the average was a hundredth of that in the sun.

TABLE 8. DATES OF BLOOMING IN THE SOIL-PIT SERIES

SPECIES	LOAM	SAND	CLAY
<i>Agrostemma githago</i> - - - -	4/25	5/26	5/10
<i>Antirrhinum hispanicum</i> - - -	5/ 7	5/15	5/20
<i>Chrysanthemum coronarium</i> - -	3/20	3/25	4/ 2

Clarkia rhomboidea	-	-	-	-	4/20	4/25	5/ 5
Gilia tricolor	-	-	-	-	2/15	3/22	2/15
Phacelia grandiflora	-	-	-	-	2/15	2/26	3/15
Raphanus sativus	-	-	-	-	1/28	3/15	2/26
Stipa leucotricha	-	-	-	-	3/10	3/30	4/30
pulchra	-	-	-	-	3/ 5	3/20	4/25
Triticum aestivum	-	-	-	-	4/15	4/20	4/18
Verbena prostrata	-	-	-	-	5/ 9	5/22	5/11

With a single exception, flowering occurred first in the well-fertilized garden loam, to the extent of one to several weeks, and this was equally true of the larger number of species not listed, owing to their failure to bloom in sand. Both available water and nutrients were most favorable in this soil for rapid growth and consequent production of flowers. There was no regularity with respect to the second plot to blossom as indicated by the table, but actually this took place in the clay plots in twoscore species by virtue of the absence of flowers in the sand. The latter was by far the poorest habitat; the greater availability of its holard was more than offset by the small amount usually present and the dwarfing effect of this was strongly augmented by a minimum of nutrients. The relative significance of these factors in the three kinds of soils is brought out clearly by the ratio of dry weights in grams. For *Agrostemma githago* which blossomed in the sand, this was 22:3:0.6; for *Gilia capitata* which did not flower, it was 19:4:0.05. This difference in behavior was even more strikingly displayed by *Madia elegans*; for the two years in which sand permitted flowering the ratios were 25:9:1 and 16:11:6, while for the two succeeding years, they were 8:4:0.08 and 12:9:0.09.

TABLE 9. DATES OF BLOOMING IN LENGTH-OF-DAY SERIES

SPECIES				L-D	M-D	S-D
Antirrhinum hispanicum	-	-	-	4/23	5/ 2	5/27
Chrysanthemum coronarium	-	-	-	2/31	3/23	3/31
Cosmos bipinnatus	-	-	-	4/ 1	4/15	4/29
Matthiola incana	-	-	-	3/15	3/24	4/ 7
Phacelia grandiflora	-	-	-	3/17	3/31	4/20
Raphanus sativus	-	-	-	1/28	2/ 6	2/28
Trifolium pratense	-	-	-	4/10	4/25	5/14
Triticum aestivum	-	-	-	4/15	5/ 2	5/12
Verbena prostrata	-	-	-	5/ 5	5/12	5/28

The full or long-day exposure ranging from 13 to 14 hours produced the earliest blossoming in every instance and this was true likewise of more than a score of species that did not come to bloom in the short-day period of 5 hours. In current terminology, some of these are "long-day" and others "short-day" plants, but all bloom during short



days at Santa Barbara, in the garden proper as well as in both tents and sheds of the photoperiod series. In general, the response in growth and flowering for both of these was similar to that in the lath-houses, though stems were shorter and leaves larger, while dry weights varied much less. This difference in behavior is to be ascribed primarily to much smaller variations in radiation due to the common exposure to the higher intensities about the daily meridian.

#### BEHAVIOR IN ACCLIMATIZATION

**Nature and Scope.**—For the most part the word acclimatization belongs to popular rather than scientific usage, and even in the latter it has never been properly defined. Recognition of this fact led to the introduction of the term *ecesis* to denote the complete process of making a new home, regardless of the factors concerned. In consequence, adjustment to a different climate was included in it, and acclimatization as a definite subprocess responsive to climate began to emerge clearly only with the rise of the climax idea. In its most striking expression it operates between two climax climates and particularly between two such extremes as prairie and tundra. In nature, this takes place rarely if ever through migration in latitude, but during great climatic shifts it has occurred where open valleys connect alpine summits with the mixed prairie of the Great Plains. The outstanding instance of this sort is furnished by Pikes Peak with its unique compensating dissection and a valley less than five miles long between the two climaxes. The exchange is facilitated by the opposing migration pathways of the two valley slopes, the warm-dry southerly one or xerocline leading up and the cool-moist northerly mesocline trending downward. This constitutes a kind of topographic ecotone that has much in common with the normal climatic one between true prairie and deciduous forest on the east, and mixed prairie and montane coniferous forest on the west.

The difficulty of movement and consequent acclimatization is obviously less between two associations of the same climax than it is between two climaxes. It decreases steadily as climatic differences diminish between faciations and is still less where two lociations meet. These mark climatic divisions of the fourth degree and hence pass readily into edaphic complexes or *eces*, where control by soil factors outweighs that of climate for a longer or shorter time. The corresponding areas may range from a great proclimax of a hundred thousand square miles, such as the sandhills of Nebraska, to a river-dune

an acre in size. A similar group comprises the disclimaxes of all sorts in which the habitat is appreciably modified by the agent of disturbance. An outstanding example of this type is presented by the "Dust-Bowl," in which soil drift and silt storms produced new edaphic conditions far beyond the collecting fields scoured by the wind.

• In all these instances, successful ecesis was the outcome of adaptation in a certain degree, sometimes in terms of function and growth, at other times in connection with behavior and form. However, at present acclimatization results almost wholly from the introduction and extension by man of species from one climax or a subdivision of it to another, principally because of the distances between them. To achieve permanence, such transfers demand a considerable amount of compensation, which is determined by the respective climates on one hand and by life-form and species on the other. This compensation may be complete, as with cultivated plants, so that no adjustment is required and hence no adaptation is called forth. Outside of the tropics, however, the rule is that winter or a rainless summer is involved, as in the studies described below. A partial amelioration at least is indispensable and this is regularly supplemented by some visible modification of behavior, form or structure.

**Survival Value.**—While survival is a necessary feature of ecesis and acclimatization, not all survival contributes to these. It must be complete to the extent of producing new individuals and typically among spermatophytes by means of seeds. However, the latter are not indispensable, as viviparous species demonstrate in a number of cases, while such geophytes as *Erythronium americanum* and *albidum* multiply chiefly by means of bulbs or corms. The absence of flowers is characteristic of the family *Lemnaceae*, yet multiplication and migration proceed regularly. But when species that flower normally, even though once in a life-span, fail to do so, survival may continue for many years in the case of what may be termed facultative non-bloomers. This consequence is not at all rare under adaptation to reduced light intensity and probably can be induced in most species by exposure to values of 1 to 10 percent. A striking illustration has been supplied by the mock-orange (*Philadelphus coronarius*), grown in a moist canyon with a cold-air stream. In the course of two decades this has been transformed into a clamberer nearly 25 feet tall, which produced a few flowers in the hottest summer of record.

In default of experimental evidence, it has been loosely assumed that most specific criteria, for example, represent structures that possess survival value. This subject will be discussed with some fulness in a later volume, but it must be emphasized here that experiment alone can determine such values. The doctrine of natural selection has made such assumptions imperative as an article of faith, though proof of the survival role of minute variations has never been forthcoming. The criteria for the species of Linnaeus, Bentham, Gray and their modern followers were drawn mainly from reproductive structures, the importance of which resides chiefly in the process of multiplication. Even the pappus of composites, which is of paramount significance in taxonomy, is a correlation phenomenon and in most cases without functional value. By contrast, the root leads all other organs in ensuring survival over dry-hot periods and the bud in making persistence possible through seasonal rest periods of winter or summer. Height and spread often follow closely and in some cases at least are equalled by the type of leaf. On the other hand, hairs have been much overrated by physiologist and systematist alike and are first to be evaluated as responses to factors rather than in teleological terms.

In considering selection in nature, it is essential to understand that this has little in common with the art of the plant-breeder. If such a process may be said to exist, it differs little if at all from adaptation. In the large number of experiments made for this purpose, survival of the population has proved to be complete or nearly so, accidents excepted, or all the individuals succumb in default of conditions that permit adaptation. Thus adaptation and correlated survival are the rule for the lath-houses with 65, 35 and 20 percent light-intensity and for the shelter garden at the dunes, while just the reverse applies to light values of 10 and 5 percent and to the ridge garden in mobile sand. In general, the range of modification lies within the limits of the species or lineage, but it not infrequently oversteps these to produce a new unit or to bring about conversion into a related one.

**Climaxes and Experimental Materials.**—The climates of the clisere at Pikes Peak are all characterized by cold winters with some subzero temperatures and by summer rains increasing in amount from plains to summit with a concomitant decrease in temperature. At Santa Barbara the climate utilized is essentially a subtropical one marked by rainless but moderate summers, and winters with few nights below

freezing. The test of survival is provided by winter in the one case and by the exceedingly dry summer in the other, in so far as reciprocal transfers are concerned. However, transplanting to higher altitudes is less difficult by reason of heavier precipitation, while movement to lower ones demands compensation by water, except in the wettest seasons. A similar relation exists between mountains and lowland in California, though the gradient is less pronounced, while desert species find both water and temperature more favorable in the coastal region.

As a consequence, some degree of water compensation, direct or indirect, is imperative for practically all species introduced from climates with summer rain. Naturally, this is accomplished mainly by watering, but shade, soil, and fertilizer have also been employed to reduce effectively the rate of transpiration or increase the absorption. Hence, few species from forest or prairie climaxes or moist seral ones have received the full impact of the subtropical climate and the acclimatization is but partial in character. By a surprising contrast, a number of species have become fully established and some have run wild on the dunes, without compensation during the long period of dryness. At the other end of the scale stands a considerable number of species that have persisted in the shade without blooming, sometimes for as much as a decade.

TABLE 10. ACCLIMATIZATION EXPERIMENTS AT SANTA BARBARA

## 1. SPECIES FROM TEMPERATE OR COLD CLIMATES

## TREES AND SHRUBS

## IN SUN

*Acer negundo*  
*Amorpha fruticosa*  
*Carpinus caroliniana*  
*Cercis canadensis*

*Fraxinus americana*  
*lanceolata*  
*Hibiscus moscheutos*  
*Philadelphus lewisi*

*Purshia tridentata*  
*Shepherdia argentea*  
*Yucca glauca*

## IN SHADE

*Chamaedaphne calyculata*  
*Cornus florida*  
*Halesia carolina*  
*Hamamelis virginiana*

*Kalmia latifolia*  
*Leucothoe catesbaei*  
*Ostrya virginiana*  
*Oxydendron arboreum*

*Pieris floribunda*  
*Robinia hispida*  
*Tsuga canadensis*

## HERBS

## ESTABLISHED FOR 10 YEARS OR MORE

## SPECIES FROM WOODLAND

*Agrimonia eupatoria*  
*Aquilegia canadensis*  
*Aster cordifolius*

*Cimicifuga americana*  
*Dicentra eximia*  
*Geum canadense*

*Geranium maculatum*  
*Phlox divaricata*

## SPECIES FROM GRASSLAND

<i>Anemone canadensis</i>	<i>Chelone glabra</i>	<i>Phlox pilosa</i>
<i>caroliniana</i>	<i>lyoni</i>	<i>Potentilla arguta</i>
<i>patens</i>	<i>Coreopsis lanceolata</i>	<i>Psoralea floribunda</i>
<i>Aster novae-angliae</i>	<i>Erigeron speciosus</i>	<i>Ranunculus acris</i>
<i>puniceus</i>	<i>Euphorbia corollata</i>	<i>Ruellia ciliosa</i>
<i>Baptisia australis</i>	<i>Lepachys columnaris</i>	<i>Solidago canadensis</i>
<i>tinctoria</i>	<i>Liatris spicata</i>	<i>Thalictrum dioecum</i>
<i>Campanula rotundifolia</i>	<i>Oxalis violacea</i>	<i>polygamum</i>
	<i>Pentstemon grandiflorus</i>	<i>Viola cucullata</i>

## SPECIES FROM ALPINE TUNDRA

<i>Achillea alpina</i>	<i>Dianthus carthusianorum</i>	<i>Solidago nana</i>
<i>Armeria alpina</i>	<i>Festuca brachyphylla</i>	<i>Stellaria alpestris</i>
<i>Campanula alpina</i>	<i>Geum turbinatum</i>	
<i>Carex festiva</i>	<i>Potentilla rubricaulis</i>	

## SURVIVING FOR 1-5 SEASONS

## SPECIES FROM WOODLAND

<i>Apios tuberosa</i>	<i>Epigaea repens</i>	<i>Trillium cernuum</i>
<i>Arisaema triphyllum</i>	<i>Habenaria psycodes</i>	<i>erectum</i>
<i>Asarum canadense</i>	<i>Hepatica acutiloba</i>	<i>grandiflorum</i>
<i>Caulophyllum thalictroides</i>	<i>triloba</i>	<i>Uvularia grandiflora</i>
<i>Chimaphila maculata</i>	<i>Orchis spectabilis</i>	<i>perfoliata</i>
<i>umbellata</i>	<i>Polygonatum commutatum</i>	<i>sessilifolia</i>
<i>Cypripedium acaule</i>	<i>Sanguinaria canadensis</i>	<i>Viola canadensis</i>
<i>reginae</i>	<i>Sarracenia purpurea</i>	<i>sagittata</i>
<i>Dicentra cucullaria</i>	<i>Silene virginica</i>	

## SPECIES FROM GRASSLAND

<i>Asclepias tuberosa</i>	<i>Houstonia purpurea</i>	<i>Mertensia virginica</i>
<i>Astragalus crassicaupus</i>	<i>Hypoxis hirsuta</i>	<i>Scutellaria galericulata</i>
<i>Caltha palustris</i>	<i>Iris versicolor</i>	<i>Sisyrinchium angustifolium</i>
<i>Dodecatheon meadia</i>	<i>Lithospermum linearifolium</i>	<i>Solidago odora</i>
<i>Eupatorium purpureum</i>	<i>Lobelia cardinalis</i>	<i>Viola pedata</i>

## TABLE 11. SPECIES FROM WARM CLIMATES

## WITH SUMMER RAIN

<i>Anisacanthus thurberi</i>	<i>Cowania stansburiana</i>	<i>Vauquelinia californica</i>
<i>Bignonia stans</i>	<i>Fallugia paradoxa</i>	
<i>Chilopsis linearis</i>	<i>Salvia greggi</i>	

## WITHOUT SUMMER RAIN

<i>Adenostoma sparsifolium</i>	<i>Ceanothus cuneatus</i>	<i>Cercis occidentalis</i>
<i>Arctostaphylos bicolor</i>	<i>cyaneus</i>	<i>Pentstemon antirrhinoides</i>
<i>manzanita</i>	<i>incanus</i>	<i>breviflorus</i>
<i>pringlei</i>	<i>integerrimus</i>	<i>cordifolius</i>
<i>pungens</i>	<i>megacarpus</i>	<i>isophyllus</i>
<i>Calycanthus occidentalis</i>	<i>thyrsiflorus</i>	
<i>Carpenteria californica</i>		

In the preceding lists, bog plants like *Cypripedium* have been included with woodland species, and swamp and meadow plants such as

*Caltha* and *Mertensia* with the grassland. The woody species tested in the sun represent a close approach to full acclimatization, though they received water during critical periods in the summer. A half of them have so far failed to flower owing to their slow growth and thus lack something more of complete adjustment. *Carpinus* takes the form of a bushy shrub 10-12 feet tall and *Acer*, though tree-like, has the stature of a shrub.

The heaths have quite unexpectedly made the best adjustment to the oak shade; they are fairly normal in size and most of the plants have bloomed every year. However, the soil is not at all acid in reaction and *Leucothoe* is the only one still in excellent health. The best response has been exhibited by *Hamamelis*, which has bloomed profusely since the first year. This is doubtless because it is in the well-lighted edge, though the shade effect has been sufficient to keep the stature between four and five feet. *Halesia* and *Robinia* have flowered sparsely as slender shrubs of medium height. The remaining species are in somewhat deeper shade; they have not flowered and survive only in much reduced form.

The woodland forbs have maintained themselves in the protection of shade with the help of an occasional watering during the dry season. Those from the grassland have been tested in both sun and shade, the first naturally requiring much more water to meet the needs of transpiration and the second calling forth structural responses to light intensity of about 20 percent. These regularly took the form of slender unbranched stems, broad thin leaves and reduced inflorescences and flowers. Blossoming usually occurred several weeks later and in several instances was entirely suppressed, notably in *Anemone caroliniana* and *Geum canadense*. On the contrary, species from the woodland shade were modified in the sun. *Solidago canadensis* exemplified the tendency of sun herbs to become woody in the shade, with rosettes of leaves at the tips of branches.

To insure their survival without excessive watering, the alpine transplants were grown in half-day (afternoon) shade. Under such conditions they maintained the dwarf habit of the alpine tundra. All of them bloomed with the exception of *Carex* and *Festuca* and 5-6 months earlier than the normal habit.

The species that persisted for but a few years were largely the geophytes of shady deciduous woods, with a preference for deep rich leaf-mold. With the exception of a few bog plants, they were tested

in a habitat as nearly similar as possible, but watering did not provide adequate compensation for the dry season and they became less and less vigorous, and finally succumbed. The behavior of the grassland species was not very different, though they had the benefit of both water and shade. For the most part they flourish in a growing season rainfall of 20 inches or more or they dwell in moist edaphic situations. The survival in general was better than for the denizens of woodland, but few of them lasted beyond the fifth year.

Two striking facts are to be noted in connection with the species from warm climates. The first is that they are all shrubby in character, a feature closely correlated with the kind of climate. The second is that a minimum of watering has permitted nearly all of them to bloom each year and some of them to spread by volunteers. The first group is derived from the Southwest where the advantage of summer rain is minimized by long seasons and high temperatures. The second is predominantly from the chaparral climax, with generally lower temperature and higher rainfall. As the results from the dunes will show even more clearly, the shrub life-form is responsible to a large degree for the relative success in acclimatization.

TABLE 12. ACCLIMATIZATION EXPERIMENTS IN COASTAL DUNES

1. SPECIES FROM TEMPERATE CLIMATES

SHRUBS

*Atriplex canescens*

*Eriogonum subalpinum*

FORBS

PERENNIALS

*Antirrhinum hispanicum*

*Pentstemon barbatus*

*Aster canescens*

*Plantago lanceolata*

*Callirhoe involucrata*

*Potentilla gracilis*

*Coreopsis lanceolata*

*Salvia argentea*

*Erigeron speciosus*

*Saponaria officinalis*

*Gaillardia hybrida*

*Splachnaceae ambigua*

*Geum strictum*

*Stanleya pinnata*

*Linum lewisii*

*Tradescantia virginiana*

*Melilotus alba*

ANNUALS

*Anagallis linifolia*

*Raphanus sativus*

*Chrysanthemum coronarium*

*Rudbeckia bicolor*

*Oenothera biennis*

*Verbesina encelioides*

*rhombipetala*

GRASSES

*Agropyrum spicatum*

*Elymus condensatus*

*Andropogon gryllus*

*Panicum virgatum*

*Aristida purpurea*

## 2. SPECIES FROM WARM CLIMATES

## SHRUBS

<i>Anisacanthus thurberi</i>	<i>Penzigia incana</i>
<i>Dasyllirion wheeleri</i>	<i>Psilostrophe cooperi</i>
<i>Encelia californica</i>	<i>Venegasia carpesioides</i>
<i>farinosa</i>	<i>Yucca elata</i>
<i>Fouquieria splendens</i>	<i>Zauschneria californica</i>
<i>Nolina parryi</i>	

## FORBS

<i>Abronia latifolia</i>	<i>Oenothera drummondii</i>
<i>Aster spinosus</i>	<i>hookeri</i>
<i>Baileya multiradiata</i>	<i>b-lanceolata</i>
<i>Eschscholtzia californica</i>	<i>trichocalyx</i>
<i>Godetia quadrivulnera</i>	<i>Sisyrinchium bellum</i>
<i>Linaria maroccana</i>	<i>Verbena prostrata</i>

## GRASSES

<i>Andropogon saccharoides</i>	<i>Stipa gigantea</i>
<i>Elymus condensatus</i>	<i>hyalina</i>
<i>Koeleria cristata</i>	<i>pulchra</i>
<i>Oryzopsis miliacea</i>	<i>p-gracilis</i>
<i>Sporobolus wrightii</i>	<i>speciosa</i>

In view of the severity of conditions on the dunes, the number of species that continue to persist is surprising. However, a comparison of results in the mobile sand of the ridge with those for the stable sand of shelter and knoll gardens affords a satisfactory explanation. The former permits rain to enter and move downward so readily and to evaporate from the upper layer so quickly that it leaves but little in the zone of roots. In the shelter garden especially the fine particles of organic material hold water on and near the surface, but the chief factor is the water-table which is near the top during the rainy winter and spring, but then drops so gradually that the roots of most of the shrubs and vigorous perennials keep pace with its withdrawal, to considerable depths at least (Martin and Clements, 1939).

The lower transpiration of woody shoots is another feature of the adjustment, especially when this is accompanied by reduction in the number and size of leaves. Moreover, the majority of the forbs, whether perennial, biennial or annual, exhibit a definite tendency to develop woody stems much better adapted to water economy. The sole perennial survivors on the ridge are five low woody shrubs, three of them monocotyls, *Dasyllirion*, *Nolina*, and *Yucca*, and two reduced undershrubs, *Gaillardia* and *Zauschneria*. A few annuals evade drouth by compressing the life-span into the rainy season when not blown out by the wind. This takes place likewise in the shelter garden, but here most of the annuals and biennials become short-lived woody perennials



lasting but two or three seasons. The larger grasses display a similar modification, the new green shoots coming from dry culms several years old. The subject of the change of life-form in the course of adaptation, to subtropical conditions especially will be discussed at some length in a later volume.

**Role of Volunteers.**—The ability of a species to produce an adequate supply of seeds and to establish new plants or colonies is a partial measure of its capacity for acclimatization. While this depends primarily upon the vegetative organs, seed production and distribution determine opportunity to a large degree, especially in terms of competition. This is best illustrated by the grasses of the first group; with one exception all these produce a single seed in each spikelet and all but two have awns or hairs for dissemination. *Andropogon saccharoides* possesses both devices, *Eragrostis* has a tumbling panicle, and *Lamarckia* a tiny cluster that rolls.

The contrast between the number of species that volunteer in the main garden and at the dunes is great, but it is explained in part by the larger area with some water compensation. Germination is more difficult on the dune sand, but this is fairly counterbalanced by a general lack of competition. The grasses make a much poorer showing on the dunes, due mainly to small seedlings and the slow development of roots.

TABLE 13. ESTABLISHMENT OF VOLUNTEERS

## SANTA BARBARA GARDEN

## UP TO DISTANCES OF 100-200 FEET

<i>Andropogon gryllus</i>	<i>Linaria vulgaris</i>
<i>saccharoides</i>	<i>Linum austriacum</i>
<i>Antirrhinum hispanicum</i>	<i>Oryzopsis miliacea</i>
<i>Arctotis grandis</i>	<i>Oxalis cernua</i>
<i>Aristida purpurea</i>	<i>Plantago lanceolata</i>
<i>Cynoglossum pictum</i>	<i>Sisyrinchium striatum</i>
<i>Eragrostis lugens</i>	<i>Stipa hyalina</i>
<i>Erigeron ramosus</i>	<i>papposa</i>
<i>Lamarckia aurea</i>	<i>tortilis</i>
<i>Lepachys columnaris</i>	<i>Verbascum blattaria</i>
<i>Leptospermum rigidum</i>	<i>Verbesina encelioides</i>

## UP TO DISTANCES OF 25-50 FEET

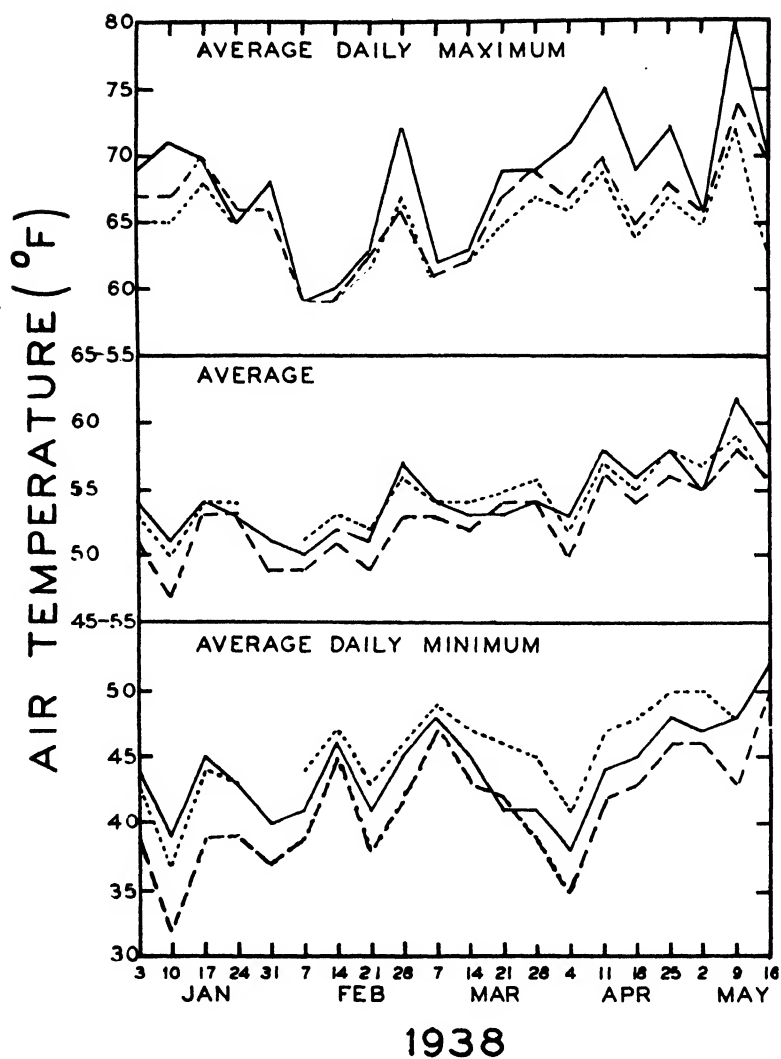
Agropyrum caninum	Geum strictum
elongatum	Malvastrum munroanum
semicostatum .	Mentha piperita
Andropogon	Oenothera spp.
Aquilegia spp.	Potentilla gracilis
Aster cordifolius	Solidago canadensis
novae-angliae	Sporobolus asper
Baileya multiradiata	poireti
Bloomeria aurea	Stipa gigantea
Callirhoe involucrata	leucotricha
Chloris ciliata	Trifolium pratense
Cooperia drummondii	Verbena urticifolia
Eragrostis curvula	

## AMONG OR ABOUT PARENT PLANTS

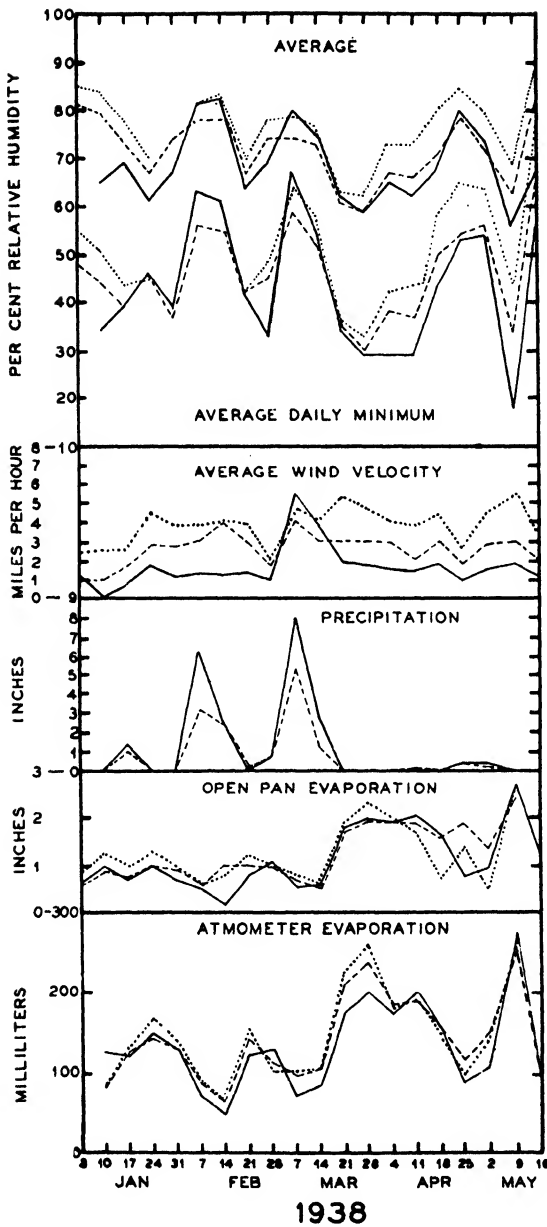
Achillea alpina	Lesquerella argentea
Allium stellatum	Oxalis violacea
Anemone canadensis	Solidago spp.
Arhenatherum elatius	Trichachne insularis
Atamosco atamosco	Veronica spicata
Buchloe dactyloides	
Elymus glaucus	SHRUBS
virginicus	
Eragrostis trichodes	Amorpha fruticosa
Gaura lindheimeri	Isomeris arborea
Grindelia blakei	Lupinus albifrons
Helianthus rigidus	Ruta graveolens
Leptochloa unanervia	Trichostemma lanatum

## COASTAL DUNE GARDEN

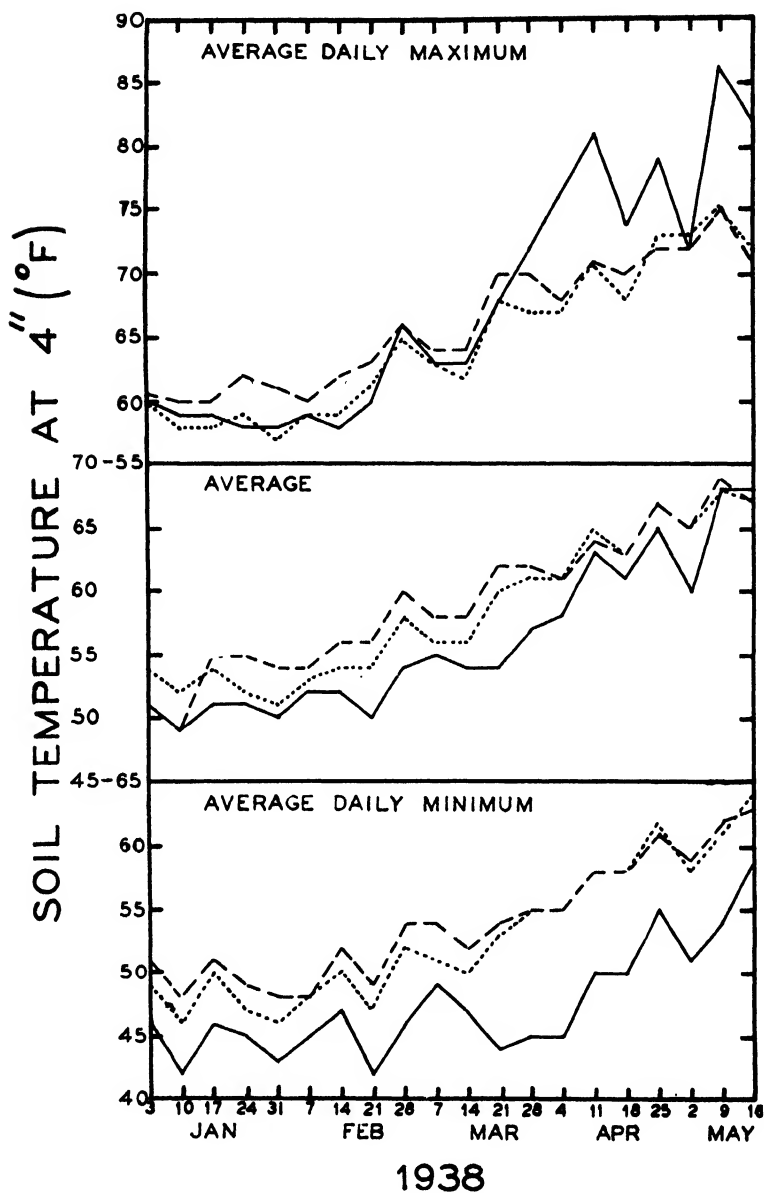
Abronia latifolia	Melilotus alba
Anagallis linifolia	Oenothera biennis
Antirrhinum hispanicum	b-lanceolata
Aristida purpurea	hookeri
Aster canescens	lamarckiana
spinosus	rhombipetala
Callirhoe involucrata	Oryzopsis miliacea
Chrysanthemum coronarium	Phacelia whitlavia
Clarkia elegans	Plantago lanceolata
Collinsia bicolor	Potentilla gracilis
Coreopsis lanceolata	Saponaria officinalis
Elymus glaucus	Stipa hyalina
Gaillardia hybrida	pulchra
Geum strictum	tortilis
Linaria maroccana	Verbesina encelioides
vulgaris	



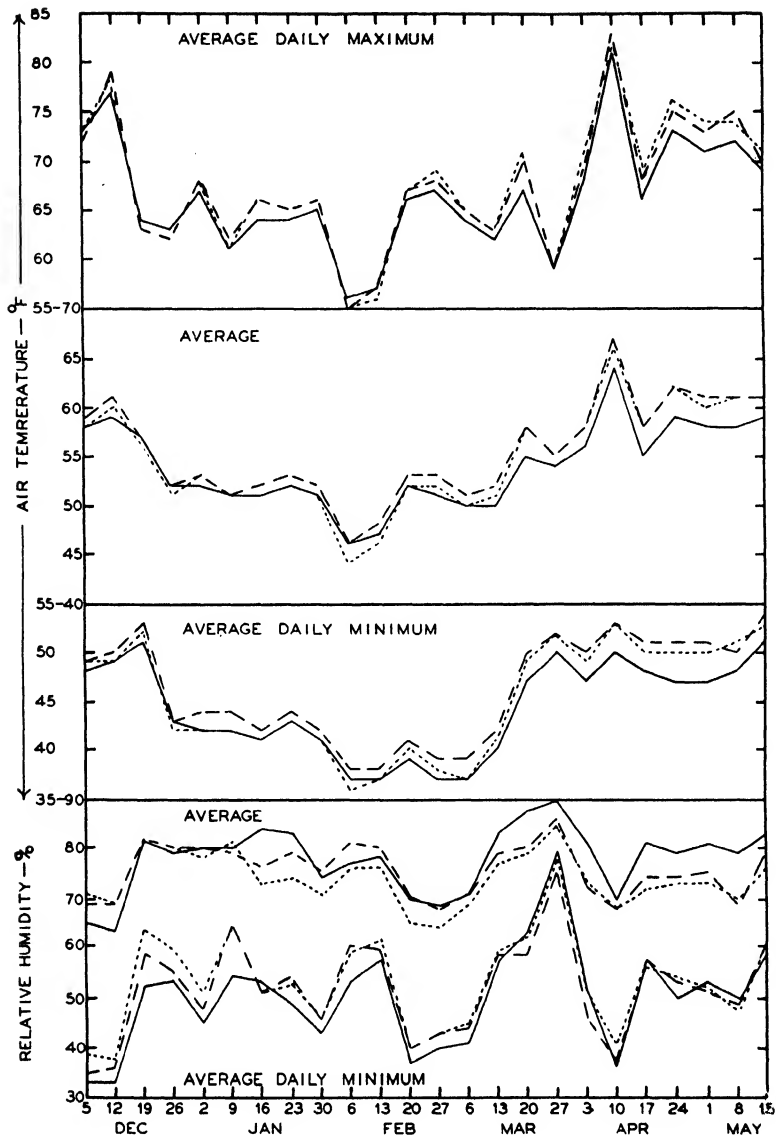
GRAPH 1. Air temperature in the Main Garden at Santa Barbara (solid line), Shelter Garden (broken line), and Ridge Garden (dotted line) for 1938.



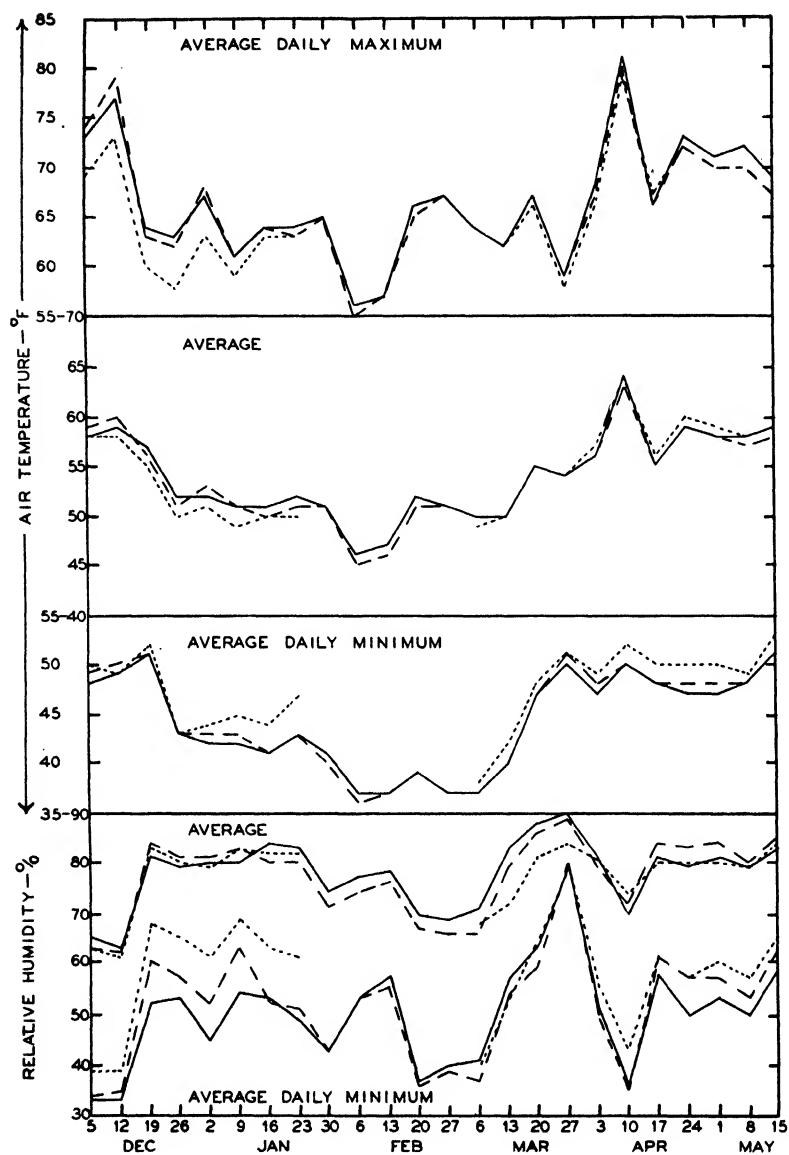
GRAPH 2. Relative humidity, wind velocity, precipitation, and evaporation in the Main Garden at Santa Barbara (solid line), Shelter Garden (broken line), and Ridge Garden (dotted line) for 1938.



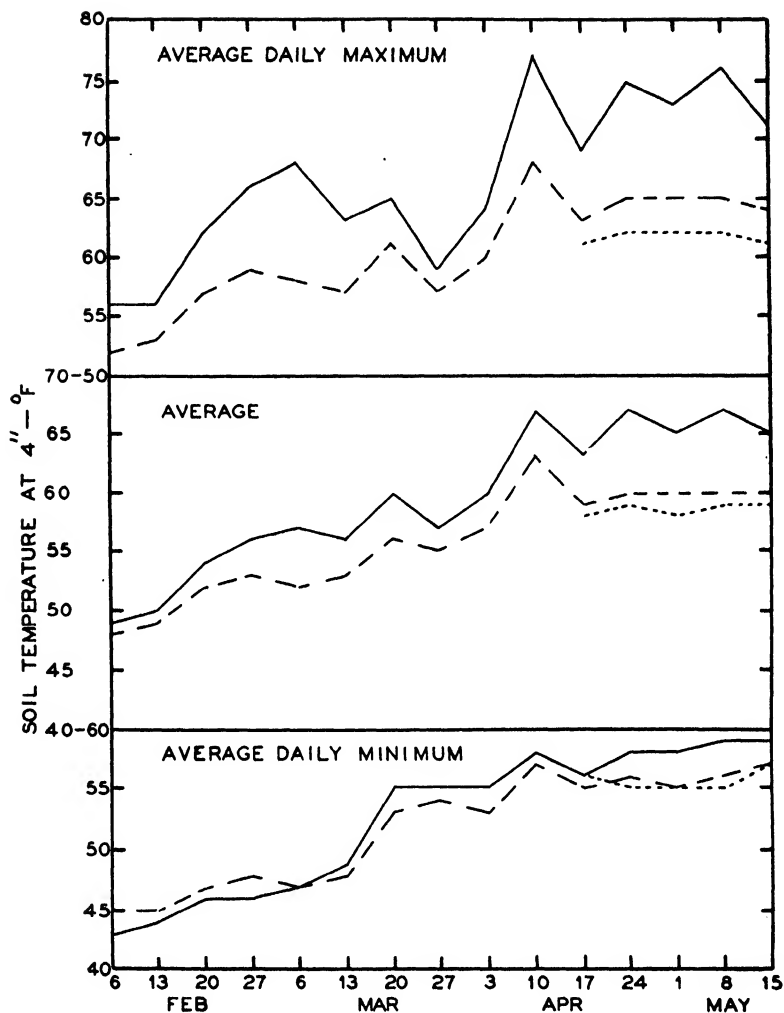
GRAPH 3. Soil temperature in the Main Garden at Santa Barbara (solid line), Shelter Garden (broken line), and Ridge Garden (dotted line) for 1938.



GRAPH 4. Air temperature and relative humidity for the season of 1938-39 for the Santa Barbara sun garden (solid line), 8½ hour-day shed (broken line), and 5 hour-day shed (dotted line).

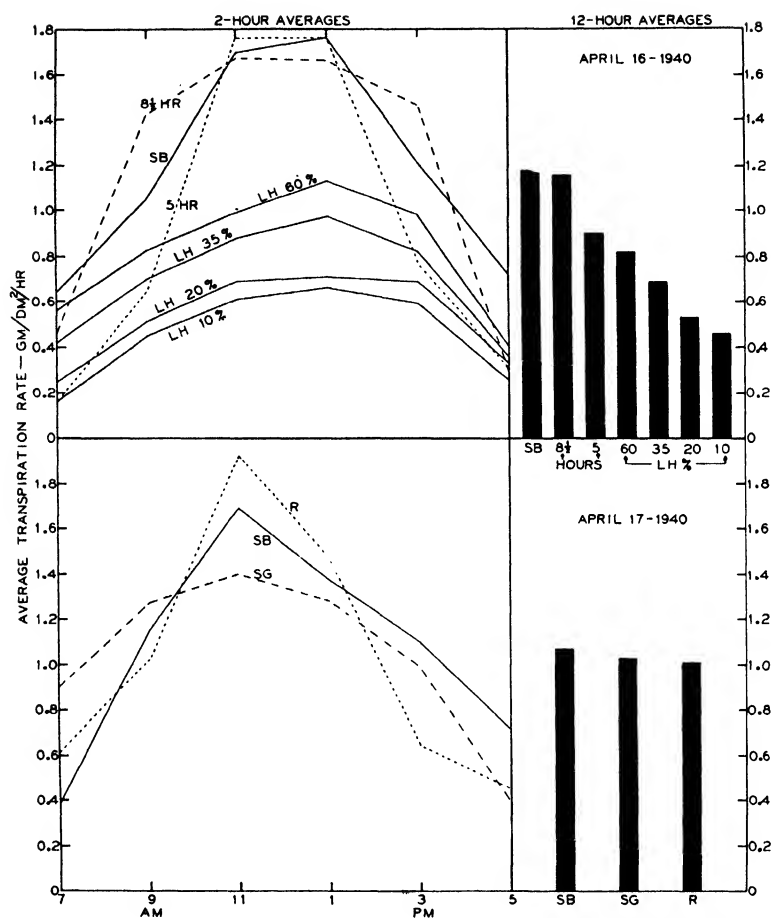


GRAPH 5. Air temperature and relative humidity for the season of 1938-39 for the Santa Barbara sun garden (solid line), lath-house 60% (broken line), and lath-house 20% (dotted line).

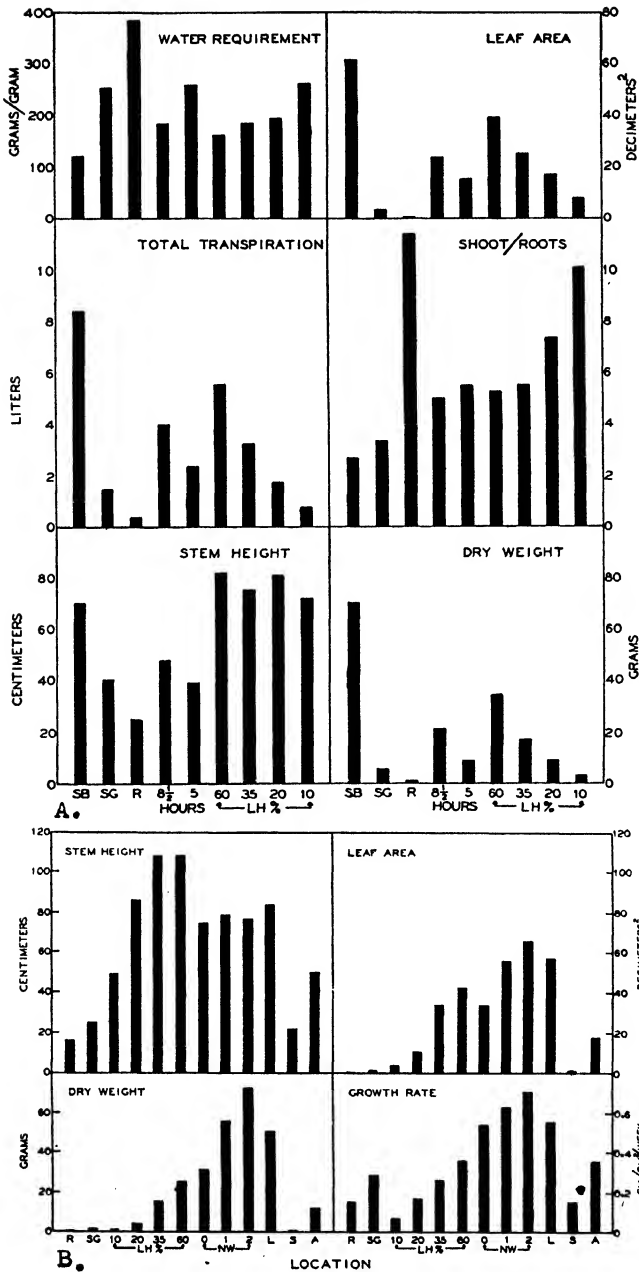


GRAPH 6. Soil temperature at depth of 4 inches for the season of 1938-39 in the Santa Barbara sun garden (solid line), lath-house 60% (broken line), and lath-house 20% (dotted line).



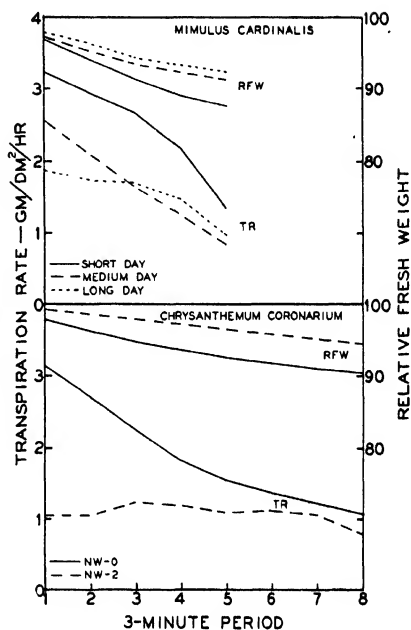
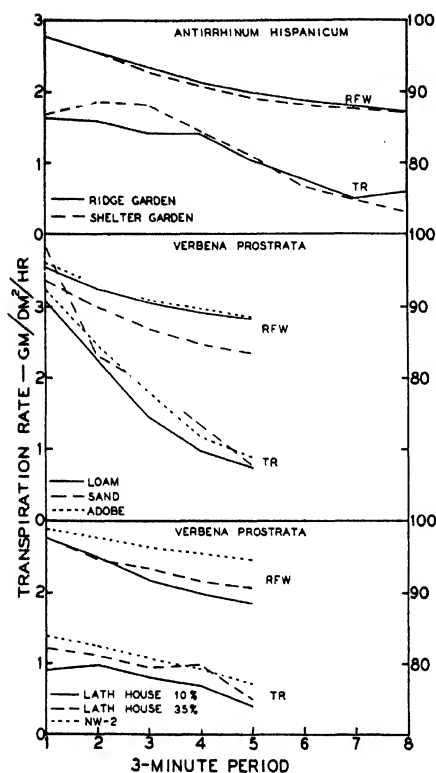


GRAPH 7. Rates of transpiration of sealed *Helianthus annuus* phytometers in a short-period series for one day with weighings taken every 2 hours. SB stands for Santa Barbara sun garden, SG for the Shelter Garden, R for the Ridge Garden, 5-hr. and 8½-hr. for the two length-of-day sheds, and LH for the lath-houses with the percentages of full sunlight shown on the curves.



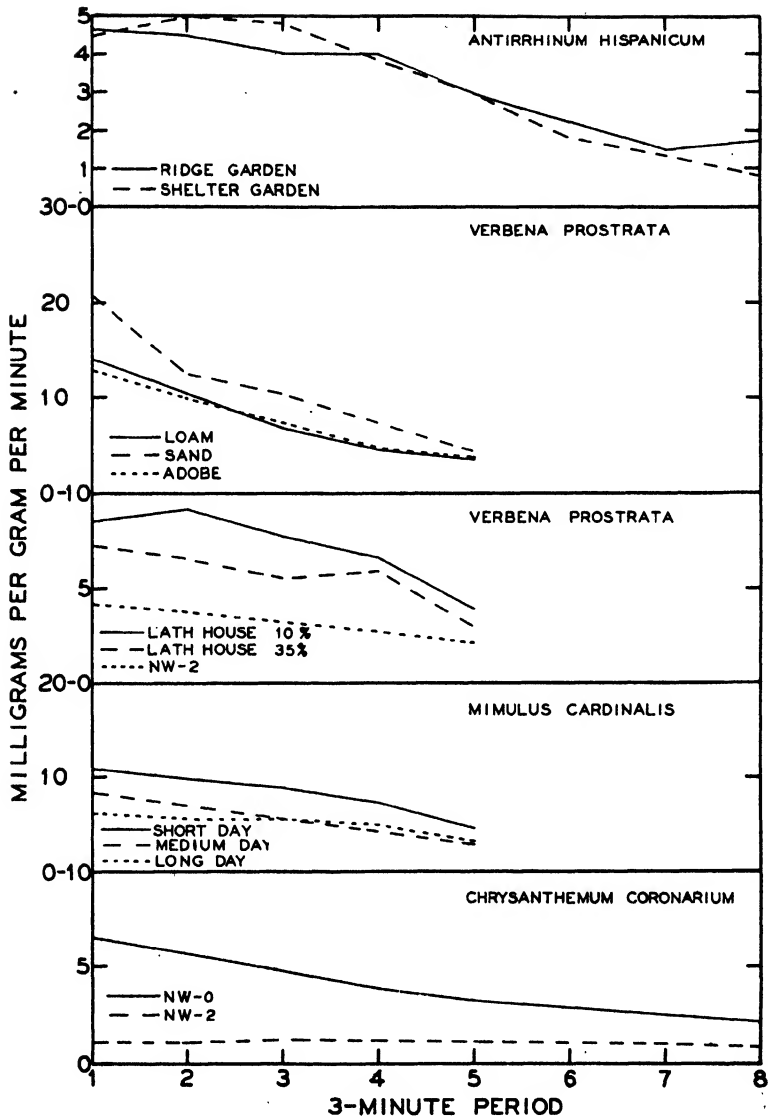
GRAPH 8. Final measurements of *Helianthus annuus* phytometers run in the spring of 1940. SB: Santa Barbara sun-garden; SG: Shelter Garden; R: Ridge Garden; 5½ and 8½ hours: length-of-day sheds; LH: Lath-houses; NW: Nutrient and water; L: Loam; A: Adobe; S: Sand.

A. Sealed Phytometers      B. Free Phytometers



GRAPH 9. Rates of transpiration (TR) of cut shoots and rate of decline of fresh weight (RFW) for plants of *Antirrhinum hispanicum* and *Verbena prostrata* grown in the locations indicated in the graphs.

GRAPH 10. Rates of transpiration (TR) and rate of decline of fresh weight (RFW) of cut shoots of plants of *Mimulus cardinalis* and *Chrysanthemum coronarium* grown in the habitats shown in the graphs.



GRAPH 11. Rates of transpiration of cut shoots expressed in milligrams per gram of fresh weight per minute for the same sets of plants and shoots shown in graphs 9 and 10.

GRAPH 12 has been renumbered 8B and will be found on page 107.

## ADAPTATION AND ORIGIN IN THE PLANT WORLD

Table 1. Soil moisture content in percentage of the dry weight of the soil (holard) in various habitats in the adaptation gardens at Santa Barbara during the spring of 1940.

Habitat	Depth 4 inches									
	Date									
	3/11	3/18	3/25	4/1	4/8	4/15	4/22	4/29	5/6	5/13
Lath house 10%	14.5	15.8	15.3	17.3	16.1	12.3	10.3	15.2	12.8	11.5
Lath house 20%	15.6	13.7	12.2	16.2	13.8	10.9	9.8	15.3	13.9	10.4
Lath house 35%	14.5	15.9	12.4	15.4	14.2	13.4	9.1	14.8	13.7	8.0
Lath house 60%	14.0	12.7	11.9	18.9	12.6	10.7	8.4	14.1	13.0	11.7
NW-0	12.2	11.4	11.1	16.3	13.0	9.1	8.8	12.2	8.7	7.8
NW-1	12.1	12.4	11.2	15.9	11.5	8.6	7.8	13.1	8.6	6.2
NW-2	11.1	12.7	11.3	15.5	12.3	7.9	8.2	12.7	8.0	6.4
Loam	13.6	12.6	13.1	18.5	13.4	10.0	10.1	14.6	9.2	7.9
Sand	3.0	4.4	4.0	4.8	4.5	3.9	4.3	4.5	4.1	2.8
Adobe	21.5	23.7	19.1	24.6	22.6	21.6	18.2	20.6	21.2	19.8
Long-day tent				17.1	12.6	7.9	11.8	14.0	10.7	7.5
Medium-day tent				18.9	13.5	9.0	10.2	16.5	11.0	8.6
Short-day tent				18.3	12.5	9.7	11.4	16.3	10.7	9.4
8-hour shed				18.7	12.9	11.8	10.2	8.5	11.7	8.9
5-hour shed				17.0	14.3	12.7	11.0	10.8	13.0	11.0
Ridge garden	3.6	3.5	2.9	5.0	3.1	3.1	3.4	4.5	3.5	3.3
Shelter garden	3.0	2.5	3.3	4.2	2.7	2.2	2.6	3.2	1.1	1.7

Habitat	Depth 12 inches									
	3/11	3/18	3/25	4/1	4/8	4/15	4/22	4/29	5/6	5/13
Lath house 10%	14.9	15.8	13.5	17.4	17.0	14.5	11.6	13.3	14.2	12.7
Lath house 20%	14.4	15.7	12.4	16.7	14.9	12.5	12.2	13.2	14.1	12.0
Lath house 35%	15.5	14.1	12.4	16.6	13.5	13.8	9.3	11.3	13.1	9.1
Lath house 60%	14.8	15.4	12.1	15.5	15.7	15.8	9.6	10.8	15.2	13.1
NW-0	13.5	13.2	13.0	15.1	14.0	10.7	10.1	10.9	11.0	9.5
NW-1	12.9	14.0	12.7	15.2	13.5	9.3	8.9	12.3	11.4	8.4
NW-2	13.2	13.8	12.5	14.8	13.3	10.0	9.1	11.5	10.2	7.3
Loam	14.3	14.1	13.5	16.3	13.8	11.1	9.3	14.0	9.7	10.2
Sand	3.6	4.1	4.2	5.1	4.5	4.4	4.2	4.4	4.5	3.5
Adobe	21.7	22.2	20.7	21.8	23.0	22.1	16.0	21.0	19.6	20.8
Long-day tent				16.1	13.8	9.8	11.9	13.8	13.7	8.4
Medium-day tent				16.0	14.5	10.6	10.9	14.3	13.3	9.1
Short-day tent				17.8	14.8	11.0	11.5	16.2	13.1	10.7
8-hour shed				15.2	13.1	12.7	11.3	8.8	10.0	9.2
5-hour shed				15.7	14.5	13.2	11.9	11.4	12.4	11.5
Ridge garden	3.5	3.8	3.6	5.8	3.9	3.3	3.7	4.7	3.9	3.8
Shelter garden	4.4	4.5	3.7	3.9	3.5	3.2	2.9	3.9	3.4	2.7

Table 2. Mechanical analysis of the various soils used in the adaptation gardens. All values are in per cent.

Soil	Fine gravel 2-1 mm	Coarse sand 1-0.5 mm	Medium sand 0.5-0.25 mm	Fine sand 0.25-0.1 mm	Very fine sand 0.1-0.05 mm
Ridge garden sand	0.0	0.3	25.0	71.1	2.5
Shelter garden sand	0.0	0.6	30.9	66.1	1.4
Loam No. 1	0.9	8.0	10.4	20.2	15.4
Loam No. 2	1.7	8.0	11.5	25.0	17.5
Adobe	0.3	3.9	6.6	17.2	16.8
River sand	6.9	41.4	27.1	18.0	2.4

Soil	Silt 0.05-0.005 mm	Clay 0.005-0	Colloid, included in clay 0.002-0 mm	Organic matter by H <sub>2</sub> O <sub>2</sub>	Mineral matter dissolved by H <sub>2</sub> O
Ridge garden sand	0.4	0.7	0.6	0.0	0.1
Shelter garden sand	0.2	0.5	0.5	0.2	0.1
Loam No. 1	27.5	14.7	11.9	1.7	0.2
Loam No. 2	21.5	13.2	9.4	1.4	0.4
Adobe	25.3	29.0	24.4	0.6	0.3
River sand	1.7	2.2	1.5	0.1	0.2

Soil	Moisture equivalent	Field capacity	Wilting coefficient
Ridge garden sand	2.8	3.3	0.7
Shelter garden sand	3.0	3.3	0.9
Loam No. 1	14.9	12.4	4.8
Loam No. 2	13.4	14.7	5.3
Adobe	20.6	21.5	11.3
River sand	2.3	3.7	1.3

These analyses were obtained through the courtesy of the Bureau of Chemistry and Soils of the U.S. Department of Agriculture. Loam No. 1 is the soil over the greater part of the adaptation garden, while loam No. 2 is the soil designated as loam in the soil-pit series.

## TABLES

111

Table 3. Chemical analysis of the various soils used in the adaptation gardens. All values are in per cent.

Soil	SiO <sub>2</sub>	TiO <sub>2</sub>	Cr <sub>2</sub> O <sub>3</sub>	Al <sub>2</sub> O <sub>3</sub>	Fe <sub>2</sub> O <sub>3</sub>	MnO	CaO	MgO	Na <sub>2</sub> O	K <sub>2</sub> O
Ridge garden sand	80.55	0.95	0.06	9.02	2.38	0.15	1.66	0.56	1.65	2.13
Shelter garden sand	83.23	0.58	0.08	8.21	1.68	0.10	1.16	0.41	1.55	2.20
Loam No. 1	73.22	0.44		13.25	2.34	0.07	0.85	0.60	2.24	3.19
Loam No. 2	73.02	0.43		13.02	2.49	0.06	1.16	0.70	2.43	3.18
Adobe	69.70	0.52		13.30	3.50	0.07	2.76	1.24	2.04	2.40
River sand	77.42	0.26		11.79	1.47	0.04	1.75	0.46	2.52	3.18
Soil	P <sub>2</sub> O <sub>5</sub>	SO <sub>3</sub>	Ignition loss	Total	Nitrogen	Nitrate	CO <sub>2</sub>	Organic matter		
Ridge garden sand	0.15	0.04	0.40	99.70	0.01	0.01	0.0	0.14		
Shelter garden sand	0.11	0.07	0.59	100.06	0.02	0.00	0.0	0.32		
Loam No. 1	0.12	0.09	3.57	99.95	0.10	0.00	0.0	2.08		
Loam No. 2	0.12	0.10	3.31	100.02	0.10	0.00	0.0	2.06		
Adobe	0.23	0.05	4.24	100.05	0.06	0.01	0.94	1.23		
River sand	0.07	0.11	0.95	100.05	0.02	0.01	0.62	0.10		

These analyses were obtained through the courtesy of the Bureau of Chemistry and Soils of the U.S. Department of Agriculture. Loam No. 1 is the soil in the general adaptation garden, while loam No. 2 is the soil designated as loam in the soil-pit series.

Table 4. Average transpiration rates in grams per square decimeter per day of *Helianthus annuus* sealed phytometers grown in the spring of 1940.

Habitat	Week ending							Average
	3/11	3/18	3/25	4/1	4/8	4/15	4/22	
Ridge garden	20.8	13.7	8.7	6.7	11.9	21.1	12.3	13.6
Shelter garden	24.6	14.7	9.9	6.6	11.2	17.6	11.0	13.7
Santa Barbara sun	17.4	13.0	6.8	6.0	9.8	10.6	4.4	9.8
Lath house 60%	13.1	12.2	6.1	5.4	7.4	8.9	6.7	8.5
Lath house 35%	9.8	10.3	5.0	4.9	6.2	7.1	8.2	7.4
Lath house 20%	7.1	8.2	4.2	2.9	4.5	5.1	6.4	5.5
Lath house 10%	4.8	6.3	3.4	1.9	3.8	3.9	6.0	4.3
8-hour shed	14.1	11.7	6.8	4.4	7.7	10.4	6.1	8.7
5-hour shed	14.8	13.8	5.8	2.1	6.0	8.9	4.8	8.0

Table 5. Final measurements of sealed phytometer series plants of *Helianthus annuus* (3-490) grown in various habitats at Santa Barbara during the spring of 1940. All values are averages. S.B. means Santa Barbara.

Habitat	Leaf area dm <sup>2</sup>	Stem		Total dry weight gm	Shoot Roots	Shoot % water	Total transpiration gm	Water require- ment gm/gm	No. of leaves	No. of plants
		Ht. cm	Diam. cm							
Ridge garden	0.62	25	0.39	1.05	11.4	84.3	394	385	7	16
Shelter garden	3.68	40	0.62	5.93	3.3	82.8	1490	254	10	10
S.B. sun	60.8	70	1.9	49.1	2.7	84.6	8410	120	29	2
Lath house 60%	39.6	82	1.4	34.6	5.3	86.6	5614	162	24	8
Lath house 35%	25.0	75	0.95	17.7	5.6	86.6	3254	184	21	8
Lath house 20%	16.9	81	0.82	9.80	7.4	86.6	1781	194	21	8
Lath house 10%	8.0	72	0.67	3.10	10.1	89.4	809	258	17	8
8-hour shed	23.5	48	1.11	21.7	5.0	85.9	3981	183	23	8
5-hour shed	15.7	39	0.84	9.80	5.6	86.6	2382	259	22	8

Table 6. Summary of ratios of transpiration rates per unit area of leaves of cut shoots of plants grown in various habitats in the adaptation gardens at Santa Barbara during the seasons of 1939-40 and 1940-41.

Species	NW-0 NW-2		NW-1 NW-2		LH 10% NW-2		LH 35% NW-2		Ridge G. Shelter G.	
	1	2	1	2	1	2	1	2	1	2
<i>Antirrhinum hispanicum</i>	0.98	0.88			0.98	0.83	1.41	1.24	0.65	0.71
<i>Chrysanthemum coronarium</i>	1.92	1.78	1.29	1.27	2.70	2.61	2.70	2.12	0.88	0.84
<i>Oenothera trichocalyx</i>	0.97	0.99	1.00	0.99	0.54	0.54	1.01	0.94	1.00	1.06
<i>Mimulus cardinalis</i>	2.28	4.40	1.40	1.89	3.07	4.05	3.07	3.26		
<i>Verbena prostrata</i>	2.12	1.48	0.84	0.84						
<i>Agrostemma githago</i>	1.47	1.87	1.53	1.70	1.53	2.56	2.04	2.85	0.86	0.74
<i>Rudbeckia bicolor</i>	2.97	2.74	1.87	1.69	1.60	1.81	1.84	1.68	1.06	1.28
<i>Gaillardia hybrida</i>									0.87	0.85
Species	Sand Loam		Adobe Loam		Short day Long day		Medium day Long day		In Out	
	1	2	1	2	1	2	1	2	1	2
<i>Antirrhinum hispanicum</i>	1.39	1.35	1.25	1.39	1.07	1.00	1.09	1.01	0.58	0.58
<i>Chrysanthemum coronarium</i>									0.69	0.79
<i>Oenothera trichocalyx</i>	1.29	1.48	1.09	1.12					0.50	0.45
<i>Mimulus cardinalis</i>			1.49	1.72	1.52	1.44	1.33	1.26	0.57	0.60
<i>Verbena prostrata</i>			1.03	1.10	0.97	1.03	0.95	1.11		
<i>Agrostemma githago</i>									0.66	0.75
<i>Rudbeckia bicolor</i>									0.37	0.39
Species	16 4		64 4		128 4		256 4			
	1	2	1	2	1	2	1	2		
<i>Arctotis grandis</i>	0.84	0.88	0.40	0.32	0.65	0.60				
<i>Helianthus annuus</i> (S-490)					0.82	0.85				
<i>Chrysanthemum coronarium</i>	1.09	1.07	0.86	0.83			0.61	0.71		
<i>Agrostemma githago</i>							0.93	0.92		
<i>Rudbeckia bicolor</i>	1.04	1.21	0.39	0.43	0.62	0.54				

The numbers 1 and 2 indicate the first and second three-minute intervals respectively. The ratios are the average of four independent comparisons, with the following exceptions. *Agrostemma githago*, Ridge garden/shelter garden, was obtained from 2 comparisons, *Oenothera trichocalyx* ridge/shelter garden from 3, *Mimulus cardinalis* in/out from 3, *Rudbeckia bicolor* in/out from 2, and *Helianthus annuus* 128/4 from 6. The numbers 4, 16, 64, 128, and 256 represent the number of individuals per square meter in competition quadrats.

## 113

Species	Source	Initial fresh weight	Three-minute interval number							
			1	2	3	4	5	6	7	8
Agrostemma githago	Lath house 10%	0.887	1.20 98.0	1.06 96.3	1.20 94.5	1.35 92.5	1.08 90.8			
	Lath house 35%	2.030	1.74 97.5	1.59 95.5	0.87 94.2	0.63 93.4	0.69 92.6			
	NW-2	3.443	1.22 98.8	0.69 98.0	0.87 97.3	0.69 96.6	1.02 95.6			
Mimulus cardinalis	Loam	5.800	2.24 97.5	1.69 95.6	0.92 94.6	0.52 94.1	0.54 93.7			
	Adobe	3.662	2.56 97.0	1.47 95.3	0.76 94.5	0.47 93.9	0.43 93.4			
	Short day	4.610	3.24 97.0	2.94 94.0	2.67 91.5	2.18 89.0	1.35 87.7			
	Medium day	7.885	2.57 97.3	2.10 95.3	1.65 93.6	1.26 92.3	0.86 91.4			
	Long day	4.433	1.88 98.0	1.73 96.5	1.70 94.6	1.47 93.4	0.97 92.5			
	Lath house 10%	1.747	2.65 98.0	1.88 91.3	1.25 88.9	0.95 87.0	0.68 85.8			
	Lath house 35%	4.015	1.03 98.5	0.35 98.0	0.50 97.7	0.23 97.3	0.28 96.9			
	NW-2	3.708	0.60 99.5	0.30 99.2	0.50 99.0	0.18 98.8	0.33 98.4			
Rudbeckia bicolor	NW-0	5.410	3.25 97.3	2.15 95.4	1.97 93.5	1.50 92.3				
	NW-1	6.784	1.80 98.6	1.23 97.3	0.81 96.6					
	NW-2	3.800	1.08 98.8	0.64 98.1	0.54 97.6	0.80 96.8				
Antirrhinum hispanicum	Ridge garden	1.503	1.63 97.6	1.59 95.4	1.40 93.5	1.40 91.4	1.03 89.8	0.79 88.8	0.51 88.1	0.61 87.3
	Shelter garden	1.961	1.68 97.7	1.87 95.3	1.83 92.8	1.45 90.9	1.11 89.3	0.69 88.5	0.49 87.7	0.31 87.4
	Lath house 10%	1.089	1.04 98.6	1.52 96.8	1.76 94.9	1.28 93.3				
	Lath house 35%	2.527	4.12 98.0	3.95 92.2	3.54 88.8					
	NW-2	4.832	3.74 98.2	3.48 96.3	3.33 94.3	2.96 92.9	2.09 91.7			
Chrysanthemum coronarum	Ridge garden	3.783	2.77 98.5	2.72 97.3	2.61 96.1	2.50 95.0	2.28 93.7			
	Shelter garden	5.503	4.33 98.1	4.14 96.2	2.95 94.7	3.31 93.2	2.69 92.2			
	NW-0	7.280	3.16 98.0	2.70 96.3	2.27 94.8	1.83 93.7	1.55 92.7	1.37 92.0	1.22 91.2	1.07 90.6
	NW-2	7.045	1.05 99.3	1.05 98.7	1.23 98.1	1.19 97.2	1.10 96.6	1.12 95.9	1.07 95.2	0.79 94.7
Verbena prostrata	Loam	2.120	3.08 95.6	2.26 92.6	1.47 90.5	0.99 89.1	0.75 88.2			
	Sand	0.321	3.84 93.7	2.31 90.0	1.92 86.8	1.35 84.6	0.77 83.5			
	Adobe	2.328	3.23 96.0	2.47 93.1	1.82 90.9	1.18 89.8	0.69 88.4			
	Lath house 10%	1.269	0.91 97.6	0.98 94.8	0.82 91.7	0.70 89.8	0.42 88.6			
	Lath house 35%	2.323	1.20 97.6	1.10 94.5	0.95 93.3	0.99 91.6	0.51 90.7			
	NW-2	3.339	1.36 98.8	1.24 97.6	1.08 96.2	0.92 95.4	0.72 94.6			

Species	Source	Initial fresh weight	Three-minute interval number							
			1	2	3	4	5	6	7	8
Agroaetasma githago	Lath house 10%	0.887	1.20 98.0	1.06 96.3	1.20 94.5	1.35 92.5	1.06 90.8			
	Lath house 35%	2.030	1.74 97.5	1.59 95.5	0.87 94.2	0.63 93.4	0.69 92.6			
	NW-2	3.443	1.22 98.8	0.69 98.0	0.87 97.3	0.69 96.6	1.02 95.6			
Mimulus cardinalis	Loam	5.500	2.24 97.5	1.69 95.6	0.92 94.6	0.52 94.1	0.54 93.7			
	Adobe	3.662	2.56 97.0	1.47 95.3	0.76 94.5	0.47 93.9	0.43 93.4			
	Short day	4.610	3.24 97.0	2.94 94.0	2.67 91.3	2.18 89.0	1.36 87.7			
	Medium day	7.885	2.67 97.3	2.10 95.3	1.65 93.6	1.26 92.3	0.86 91.4			
	Long day	4.433	1.88 98.0	1.73 96.5	1.70 94.6	1.47 93.4	0.97 92.5			
	Lath house 10%	1.747	2.65 98.0	1.88 91.3	1.25 88.9	0.95 87.0	0.66 85.8			
	Lath house 35%	4.015	1.03 98.5	0.35 98.0	0.50 97.7	0.23 97.3	0.28 96.9			
	NW-2	3.708	0.60 99.5	0.30 99.2	0.30 99.0	0.18 98.8	0.33 98.4			
Rudbeckia bicolor	NW-0	5.410	3.25 97.3	2.15 95.4	1.97 93.5	1.50 92.3				
	NW-1	6.784	1.80 98.6	1.23 97.3	0.81 96.6					
	NW-2	3.800	1.08 98.8	0.64 98.1	0.54 97.6	0.80 96.8				
Antirrhinum hispanicum	Ridge garden	1.503	1.63 97.6	1.59 95.4	1.40 93.5	1.40 91.4	1.03 89.8	0.79 88.8	0.51 88.1	0.61 87.3
	Shelter garden	1.961	1.68 97.7	1.87 95.3	1.83 92.8	1.45 90.9	1.11 89.3	0.69 88.5	0.49 87.7	0.31 87.4
	Lath house 10%	1.089	1.04 98.6	1.52 96.8	1.76 94.9	1.28 93.3				
	Lath house 35%	2.527	4.12 98.0	3.95 98.2	3.54 98.6					
	NW-2	4.832	3.74 98.2	3.48 96.3	3.33 94.3	2.96 92.9	2.09 91.7			
Chrysanthemum coronarum	Ridge garden	3.783	2.77 98.5	2.72 97.3	2.61 96.1	2.50 95.0	2.28 93.7			
	Shelter garden	5.503	4.33 98.1	4.14 96.2	2.95 94.7	3.31 93.2	2.69 92.2			
	NW-0	7.280	3.16 98.0	2.70 96.3	2.27 94.8	1.83 93.7	1.55 92.7	1.37 92.0	1.22 91.2	1.07 90.6
	NW-2	7.045	1.05 99.3	1.05 98.7	1.23 98.1	1.19 97.2	1.10 96.6	1.12 95.9	1.07 95.2	0.79 94.7
Verbena prostrata	Loam	2.120	3.08 95.6	2.26 92.6	1.47 90.5	0.99 89.1	0.75 88.2			
	Sand	0.321	3.84 93.7	2.31 90.0	1.92 86.8	1.35 84.6	0.77 83.5			
	Adobe	2.328	3.23 96.0	2.47 93.1	1.82 90.9	1.18 89.8	0.89 88.4			
	Lath house 10%	1.269	0.91 97.6	0.98 94.8	0.92 91.7	0.70 89.8	0.42 88.6			
	Lath house 35%	2.323	1.20 97.6	1.10 94.5	0.95 93.3	0.99 91.6	0.51 90.7			
	NW-2	3.339	1.38 98.8	1.24 97.6	1.08 96.2	0.92 95.4	0.72 94.6			



Table 8. Relative leaf areas per plant, relative transpiration rates per unit leaf surface, and relative transpiration per plant for *Mimulus cardinalis* grown under various conditions of semi-control in the adaptation garden at Santa Barbara.

Habitat	Relative leaf areas	Relative transpiration rates	Relative transpiration per plant
NW-0	0.29	3.30	0.96
NW-1	0.64	1.65	1.06
NW-3**	1.00	1.00	1.00
Lath house 35%	0.17	3.15	0.54
Lath house 10%	0.021	3.55	0.08
Long day**	1.00	1.00	1.00
Medium day	1.01	1.29	1.30
Short day	0.51	1.48	0.76
Loam**	1.00	1.00	1.00
Adobe	0.40	1.60	0.64

\*\* These are taken as standard habitats against which the others in the three groups indicated are compared.

Table 9. Increment in dry weight per week of *Helianthus annuus*(S-490) grown in various plats in the adaptation gardens at Santa Barbara during the spring of 1940. In the upper portion of the table the values are expressed in grams per plant per week. In the lower part values are in percentage of the dry weight at the end of the previous week.

Habitat	Week ending						
	3/18	3/25	4/1	4/8	4/15	4/22	4/29
Ridge garden	0.032	0.031	0.019	0.031	0.084	-0.012	0.106
Shelter garden	0.044	0.031	0.093	0.257	0.225	0.60	0.07
Lath house 10%	0.010	0.035	0.120	0.018	0.099	0.141	0.290
Lath house 20%	0.083	0.100	0.345	0.263	0.96	1.59	0.67
Lath house 35%	0.090	0.213	0.53	0.60	2.99	3.03	8.22
Lath house 60%	0.075	0.294	0.85	0.95	4.52	8.2	10.8
NW-0	0.106	0.357	1.22	3.24	8.5	25.4	- 7.0
NW-1	0.176	0.498	0.37	3.23	8.5	26.8	16.5
NW-2	0.197	0.644	0.74	4.44	10.1	28.9	27.1
Loam	0.118	0.289	1.56	1.57	8.7	15.8	22.3
Sand	0.076	0.052	0.034	0.250	0.10	0.90	- 0.69
Adobe	0.088	0.113	0.263	0.500	1.07	2.58	6.8
Ridge garden	39	17	13	19	33	- 5	43
Shelter garden	31	27	42	32	40	76	5
Lath house 10%	9	28	80	7	34	36	55
Lath house 20%	49	52	118	41	107	85	19
Lath house 35%	50	79	110	59	186	66	108
Lath house 60%	39	109	151	67	192	119	71
NW-0	43	102	172	168	160	188	- 13
NW-1	58	103	38	243	182	208	42
NW-2	78	152	69	245	161	176	60
Loam	50	76	250	72	231	126	79
Sand	86	32	16	100	21	150	- 46
Adobe	43	38	65	71	89	79	116

## TABLES

115

Table 10. Final measurements of plants of *Helianthus annuus* (S-490) grown in various habitats in the adaptation gardens at Santa Barbara during the spring of 1940. All values are the average of eight plants.

Habitat	Leaf area dm <sup>2</sup>	Stem		Bud Diam. cm	No. of leaves	Total dry wt. gm	Shoot Roots	Shoot % water	Growth rate gm/dm <sup>2</sup> /wk.
		Ht. cm	Diam. cm						
Ridge garden	0.18	16	0.27	0.8	5	0.35	4.6	82.3	0.158
Shelter garden	1.09	25	0.40	1.5	8	1.46	5.3	80.9	0.292
Lath house 10%	3.56	49	0.46	0.6	14	0.82	15.4	92.4	0.070
Lath house 20%	10.5	86	0.69	1.8	17	4.12	14.7	90.2	0.173
Lath house 35%	34.1	108	1.2	2.6	22	15.85	12.5	90.0	0.267
Lath house 60%	42.6	108	1.5	3.5	24	25.9	9.6	88.7	0.362
NW-0	33.9	75	1.6	5.0	19	31.9	7.1	85.7	0.539
NW-1	55.8	79	1.7	5.7	20	56.2	6.4	86.1	0.631
NW-2	66.2	77	2.3	6.6	21	72.4	5.5	86.1	0.706
Loam	57.3	84	2.1	4.6	23	50.6	6.4	86.7	0.556
Sand	1.07	22	0.37	1.0	11	0.81	5.5	84.3	0.156
Adobe	17.9	50	1.0	3.2	19	12.7	6.2	86.3	0.356

Table 11. Results of a series of measurements of the growth rate of *Helianthus annuus* (S-490) free phytometers in selected habitats at Santa Barbara in the spring of 1940. Values of growth rate are expressed in grams per square decimeter per week. Most of the values are determined from 25 plants, but none are from less than 22. S.B. means Santa Barbara.

Habitat	Mean growth rate						Final leaf area	Final dry wt.
	Week ending							
	3/21	3/28	4/4	4/11	4/18	Average		
Ridge garden	0.219	0	0.177	0.013	0.326	0.147	0.134 dm <sup>2</sup>	0.220 gm
Shelter garden	0.218	0.166	0.356	0.403	0.233	0.271	1.44	1.336
S.B. (NW-0)	0.255	0.365	0.307	0.573	0.454	0.391	36.43	28.8
S.B. (NW-1)	0.401	0.311	0.332	0.592	0.467	0.421	35.01	28.0
Lath house 20%	0.196	0.122	0.158	0.188	0.185	0.170	9.44	3.58

## 12 Number and Size of Stomata in Upper and Lower Epidermis

Habitat		Leaf Size		Upper			Under		
		L	W	No. per sqmm	L	W	No. per sqmm	L	W
		cm			mm			mm	mm
<u>Helianthus annuus Phytometers</u>									
<u>Sealed</u>									
Light	100%	18.9	16.0	142	28	25	268	28	25
	60%	16.0	13.0	142	28	21	252	28	21
	35%	16.5	13.5	110	28	21	220	32	25
	20%	12.0	8.5	95	32	21	173	32	21
	10%	11.5	7.5	79	32	25	142	32	25
8½ Hr. shed		13.0	11.0	252	28	21	315	28	21
5 Hr. shed		12.5	9.5	205	25	21	283	28	21
<u>Free</u>									
Light	60%	20.0	14.0	126	32	25	173	32	21
	35%	17.0	11.0	126	32	25	158	35	25
	20%	14.0	7.0	110	35	21	158	32	21
	10%	8.5	4.0	63	32	21	110	32	25
Loam		20.0	14.5	158	35	21	189	35	25
Adobe		12.0	8.0	158	35	21	252	32	25
Sand		5.0	3.0	236	28	25	283	32	21
NW-0		17.0	13.5	158	35	21	205	35	25
NW-1		23.0	19.0	142	32	25	205	35	25
NW-2		28.0	26.5	205	32	21	205	35	21
<u>Chrysanthemum coronarium</u>									
Light	100%	6.5	4.3	87	46	35	126	49	35
	60%	9.0	4.8	57	63	60	63	60	39
	35%	8.7	5.0	63	53	35	63	53	35
	20%	8.7	5.3	47	53	35	53	56	35
	10%	6.5	3.0	31	42	32	31	46	32
	5%	5.5	2.5	31	42	28	31	42	32
Out		5.5	3.5	77	53	35	126	53	28
In		6.5	3.5	72	42	32	78	42	32
Dominant		8.2	4.5	47	53	39	63	56	35
Suppressed		3.2	1.0	53	46	32	95	46	35
<u>Dunes</u>									
Loam		14.5	9.0	41	67	42	47	63	35
Shelter sand		5.3	3.3	47	60	35	79	63	39
Ridge sand		3.5	1.7	79	42	28	87	49	32
<u>Chrysanthemum coronarium Phytometers.</u>									
Light	100%	7.5	4.3	43	56	32	47	49	30
	60%	10.8	6.2	33	63	35	39	63	32
	20%	12.8	6.0	21	60	35	32	67	32
	5%	8.8	4.8	16	49	28	27	49	28
6-Hr. shed		7.2	4.4	47	42	32	50	49	28
4-Hr. shed		5.3	4.5	71	42	25	90	39	25
<u>Mimulus cardinalis.</u>									
Light	100%	7.5	3.5	110	32	21	142	32	25
	60%	7.0	3.6	110	34	21	156	32	25
	35%	8.4	3.8	110	28	21	162	28	21
	20%	8.7	4.8	74	28	21	96	28	21
	10%	6.5	3.0	69	32	25	85	28	21
	5%	8.0	4.0	58	28	21	77	28	21
Out		6.6	3.6	110	25	18	236	25	18
In		11.0	4.5	47	28	21	95	25	21
<u>Dunes</u>									
Shelter		3.5	1.8	110	28	21	205	28	21
Ridge		2.0	1.3	162	28	21	189	32	21

Table No. 12 Number and Size of Stomata in Upper and Lower Epidermis.

Habitat	Leaf Size		Upper			Under			
	L	W	No. per sq mm	L	W	No. per sq mm	L	W	
									cm
<u>Oenothera tricolor</u>									
Light	60%	17.6	3.5	142	28	21	158	28	21
	35%	18.6	3.5	126	32	25	142	28	21
	20%	14.0	3.0	126	28	21	136	28	21
	10%	6.5	1.0	119	28	21	123	28	21
	5%	6.0	1.0	110	28	21	120	28	21
Out		12.0	2.2	189	28	25	236	28	21
In		11.5	2.0	156	28	21	189	28	21
Dunes									
Shelter (seeds)		10.3	3.4	208	25	21	245	25	21
Shelter last yr.		11.5	2.3	126	32	21	163	28	21
Ridge		2.0	0.8	236	28	21	315	28	21
<u>Verbena prostrata</u>									
Light	60%	8.1	7.4	35	30	23	299	28	21
	35%	12.7	10.5	32	30	21	221	28	21
	20%	15.3	11.7	32	28	21	221	28	21
	10%	11.0	9.2	32	28	21	222	25	18
	5%	10.1	7.1	16	28	21	205	26	18
Long-day		8.3	6.8	32	26	18	362	25	21
Mid-day		9.4	7.1	33	25	19	350	25	21
Short-day		9.9	7.0	24	32	21	347	25	21
8½ Hr. shed		8.0	6.6	32	28	21	362	25	21
5 Hr. shed		7.3	5.6	35	25	19	325	25	18
NW-0		7.5	5.0	32	28	21	268	28	21
NW-1		7.6	6.7	32	28	18	346	28	21
NW-2		8.5	7.1	33	28	18	331	28	21
Loam		10.0	8.8	21	28	21	394	28	21
Adobe		6.4	6.0	47	26	21	425	28	21
Sand		2.1	1.6	79	25	19	425	25	18
Out		7.5	6.0	40	25	18	252	25	18
In		10.0	6.5	32	25	21	242	25	18
Dunes shelter		12.0	7.3	61	32	18	393	28	18
Dunes " shade		13.5	8.8	24	28	21	182	28	18

TABLE 13

Habitat %	Plant Height cm	Width cm	Stem Diam. cm	Leaf Length cm	Width cm	Flowers No.	Diam. cm	Weight Fresh gm	Dry gm
<u>Antirrhinum hispanicum</u>									
Sun and Shade Series									
100	62.0	43.0	1.0	5.0	1.0	33	2.4	215.0	52.0
60	70.0	47.0	0.8	5.9	1.6	14	2.4	120.0	30.0
35	78.0	18.0	0.6	6.4	1.6	4	2.4	60.0	15.0
20	83.0	42.0	0.5	6.8	1.9	3	2.4	19.0	10.0
10	60.0	10.0	0.2	5.1	1.6	0		12.0	3.5
5	65.0	15.0	0.2	5.8	2.0	0		14.0	2.3
100	46.2	34.8	0.7	5.0	0.9	27	2.5	159.0	37.5
60	57.0	19.0	0.5	6.0	1.2	10	2.5	105.0	22.9
35	54.6	19.0	0.4	6.3	1.4	7	2.5	35.0	6.7
20	63.3	20.0	0.4	6.8	1.5	4	2.4	27.0	5.0
10	34.2	14.0	0.1	3.9	1.5	0		4.2	0.7
5	50.0	11.0	0.2	5.5	1.7	0		3.3	0.5
Length of Day Series									
Long-day	44.8	30.0	0.5	5.3	1.3	26	2.6	182.0	41.2
Mid-day	49.6	35.6	0.8	5.8	1.2	10	2.5	215.0	44.5
Short-day	37.4	26.2	0.6	5.3	1.3	0		67.0	12.2
Soil Series									
Loam	66.0	34.0	0.6	4.4	1.2	43	2.4	215.0	52.0
Adobe	44.0	16.0	0.5	3.4	1.2	12	2.7	37.0	8.1
Sand	28.0	9.0	0.4	3.3	1.1	4	2.3	12.0	3.5
Loam	55.6	37.8	0.5	5.8	1.0	32	2.6	252.0	62.0
Adobe	42.2	26.6	0.4	5.1	1.2	15	2.5	135.0	30.8
Sand	17.1	12.2	0.3	3.7	0.7	7	Buds	5.4	0.9
Nutrient Series									
NW-0	36.4	22.2	0.6	4.0	0.8	6	2.4	59.0	14.0
NW-1	46.2	34.8	0.7	5.0	0.9	27	2.5	159.0	37.5
NW-2	54.0	38.8	0.8	5.7	1.3	28	2.6	242.0	56.7
NW-0	48.0	22.0	0.6	3.5	0.9	10	2.6	65.0	13.9
NW-1	67.0	30.0	0.6	4.0	1.2	23	2.5	137.0	30.7
NW-2	77.0	41.0	0.8	4.1	1.5	56	2.7	255.0	51.4
NW-0	49.0	26.0	0.8	4.3	1.2	12	2.5	100.0	25.0
NW-1	62.0	43.0	1.0	5.0	1.0	33	2.4	175.4	37.5
NW-2	79.0	48.0	1.5	5.3	1.3	53	2.5	334.7	66.9
Dune Garden Series									
Main	48.0	22.0	0.6	3.5	0.9	10	2.6	99.4	27.3
Shelter	34.0	15.0	0.4	4.3	1.7	6	2.4	34.2	2.0
Ridge	16.0	9.0	0.3	3.0	1.0	5	Buds	8.7	1.5
Main	36.4	22.2	0.6	4.0	0.8	6	2.4	59.0	14.3
Shelter	12.3	11.7	0.3	2.9	0.9	7	Buds	17.0	3.6
Ridge	6.3	4.2	0.2	2.0	0.7	0		1.9	0.6

## SPECIES TABLES

119

TABLE 13 (CONT'D)

Habitat	Plant		Stem Diam. cm	Leaf		Flowers		Weight	
	Height cm	Width cm		Length cm	Width cm	No.	Diam. cm	Fresh gm	Dry gm
<u>Chrysanthemum coronarium</u>									
Sun and Shade Series									
%									
100	62.0	42.0	1.5	7.8	4.4	20	5.6	341.8	90.3
60	82.0	49.0	0.9	7.3	3.9	48	4.9	434.2	73.3
35	83.0	42.0	0.9	7.8	4.4	25	5.0	610.0	74.1
20	77.0	25.0	0.9	7.3	3.4	9	4.3	144.0	29.3
10	71.0	11.0	0.6	5.5	2.7	1	3.3	26.4	2.9
5	51.0	18.0	0.5	5.6	2.7		Buds	9.2	0.9
100	58.0	52.0	1.3	7.1	4.2	40	5.6	730.0	140.0
60	82.0	53.0	1.0	8.4	5.0	44	5.1	600.0	80.0
35	87.0	52.0	1.1	10.7	6.2	27	5.1	680.0	85.0
20	83.0	36.0	1.0	10.3	5.8	3	4.0	355.0	42.0
10	62.0	15.0	0.7	8.4	4.3	0		55.0	3.7
5	48.0	15.0	0.6	7.0	3.8	0		17.0	1.0
Length of Day Series									
Long-day	61.0	56.0	1.5	8.2	4.8	38	6.4	740.0	167.2
Mid-day	41.0	34.0	1.0	7.7	4.1	9	6.1	196.0	45.7
Short-day	31.0	31.0	0.9	7.3	3.8	1	5.0	94.9	21.9
Long-day	49.0	47.0	1.1	5.4	2.5	44	5.2	740.0	
Mid-day	36.0	38.0	1.0	5.9	3.0	20	4.7	196.0	
Short-day	34.0	39.0	0.9	6.9	3.3	10	3.5	94.9	
Nutrient Series									
NW-0	42.0	30.0	0.9	5.8	3.2	12	4.5	145.0	31.0
NW-1	58.0	52.0	1.3	7.1	4.2	40	5.6	730.0	140.0
NW-2	54.0	65.0	1.7	7.8	4.6	99	5.7	1520.0	282.0
NW-0	37.7	28.1	0.7	5.2	2.4	9	4.8	105.0	21.7
NW-1	45.0	40.5	1.5	6.9	3.5	17	5.4	315.0	76.0
NW-2	50.9	48.9	1.8	7.4	3.8	31	5.9	512.0	122.4
NW-0	49.0	36.0	0.7	3.9	2.2	16	4.1	216.9	46.3
NW-1	64.0	38.0	1.0	5.6	3.4	26	4.5	540.5	124.7
NW-2	54.0	53.0	1.6	6.8	4.2	50	4.6	625.0	148.4
Soil Series									
Loam	68.0	68.0	2.1	7.0	3.9	87	4.9	492.2	119.5
Adobe	35.0	24.0	0.7	5.1	2.5	10	4.5	80.0	19.9
Sand	24.0	16.0	0.5	3.1	1.6	4	4.5	20.1	4.1
Loam	57.0	38.0	1.0	6.4	3.6	19	5.9		
Adobe	30.0	28.0	0.7	4.9	2.6	1	5.9		
Sand	14.9	3.7	0.2	2.0	1.1	1	4.0		
Dune Garden Series									
Main	49.0	36.0	0.7	3.9	2.2	16	4.1	216.9	49.3
Shelter	38.0	34.0	0.7	4.7	2.6	15	5.3	310.0	70.0
Ridge	17.3	3.5	0.3	2.1	0.9	1	4.9	7.5	1.7
Main	42.0	30.0	0.9	5.8	3.2	12	4.5	145.0	31.0
Shelter	41.0	45.0	0.9	7.6	4.2	22	6.2	91.1	22.0
Ridge	18.0	16.0	0.4	4.3	2.3	5	4.7	3.5	0.8
Competition Series									
							Stems No.		
4	43.0	33.0	.63	6.0	3.3	33	6.0	10	24.70
18	41.0	18.0	.52	4.7	2.4	13	5.0	5	9.55
64	49.0	12.0	.42	4.9	2.4	7	4.6	4	5.90
256	38.0	7.0	.32	3.4	1.5	3	3.1	2	1.05

TABLE 13 (CONT'D)

Habitat	Plant		Stem	Leaf		Flowers		Weight	
	Height cm	Width cm	Diam. cm	Length cm	Width cm	No.	Diam. cm	Fresh gm	Dry gm
<u>Clarkia elegans</u>									
Sun and Shade Series									
%									
100	71.1	34.6	0.7	4.0	2.0	3.5		155.8	33.6
10	91.0	28.2	0.3	7.6	2.8	4.1		26.3	4.3
5	109.2	35.1	0.3	7.5	2.7	4.1		19.7	3.0
100	85.0	55.0	1.0	2.5	1.0	90	2.7	382.0	84.0
60	142.0	60.0	1.5	4.6	1.9	118	3.3	745.0	202.0
35	168.0	63.0	1.1	5.2	1.9	59	3.5	600.0	110.0
20	184.0	64.0	0.8	7.2	2.4	48	3.6	350.0	46.0
10	133.0	26.0	0.4	5.8	2.3	21	3.6	40.0	6.0
5	115.0	24.0	0.3	5.9	2.4	9	3.3	22.0	2.6
Length of Day Series									
Long-day	75.6	39.4	0.6	4.4	1.6		3.4	63.8	15.2
Mid-day	66.3	30.2	0.6	4.9	1.8		3.0	51.3	8.4
Short-day	41.5	27.4	0.4	3.2	1.5			30.9	4.1
Nutrient Series									
NW-0	73.0	24.4	0.6	3.9	1.4		3.4	34.4	7.5
NW-1	71.1	34.6	0.7	4.0	2.0		3.5	155.8	33.6
NW-2	67.3	38.8	0.7	5.2	2.1		3.5	236.9	68.3
NW-0	68.0	32.0	0.9	3.0	1.3	29	2.6		
NW-1	90.0	41.0	1.3	3.8	1.6	75	3.1		
NW-2	94.0	42.0	1.5	3.7	1.6	85	3.6		
Soil Series									
Loam	117.5	48.2	1.0	5.1	1.8	31	2.9		
Adobe	106.5	32.2	0.8	4.7	1.7	9	3.5		
Sand	71.6	15.8	0.5	3.7	1.4	2	3.0		
Loam	64.5	34.5	0.6	5.1	1.8		3.5	79.5	20.8
Adobe	46.2	16.5	0.3	3.8	1.4		3.5	11.3	3.0
Sand	36.8	11.9	0.2	2.6	1.1			5.8	2.0
Dune Garden Series									
Main	152	59.0	0.6	8.9	3.3	16	4.1	74.0	17.3
Shelter	17.0	8.0	0.2	2.3	0.2	1	1.6		

## SPECIES TABLES

121

TABLE 13 (CONT'D)

Habitat	Plant Height cm	Width cm	Stem Diam. cm	Leaf Length cm	Width cm	Flowers No.	Diam. cm	Fresh gm	Dry gm
<u>Coreopsis lanceolata grandiflora</u>									
Sun and Shade Series									
%									
100	61.0	45.0	1.4	24.3	7.5	25	4.9	180.0	49.5
10	56.0	28.0	0.5	11.1	6.5	1	4.1	17.5	3.8
5	49.0	21.0	0.4	8.9	5.4	1	3.6	14.7	1.5
Nutrient Series									
NW-0	69.0	39.0	0.6	20.4	6.8	7	5.4	114.6	36.7
NW-1	61.0	45.0	1.4	24.0	7.5	25	4.9	180.0	49.5
NW-2	64.0	33.0	1.3	16.0	6.2	26	4.7	293.8	100.0
<u>Oenothera trichocalyx</u>									
Sun and Shade Series									
%									
100	47.0	49.0	0.9	17.7	4.4	8	7.7	211.0	46.1
60	118.0	46.0	1.0	18.1	3.2	3	7.2	129.3	31.9
35	116.0	28.0	0.7	17.6	2.4	2	6.8	119.0	16.8
20	91.0	21.0	0.6	15.3	2.2			75.8	10.2
10	28.0	10.1	0.3	9.3	1.3	0		21.4	3.1
5	8.3	8.0	0.2	5.4	0.8	0		9.3	1.3
Nutrient Series									
NW-0	40.0	41.0	0.8	18.2	3.1	3	7.1	187.0	33.0
NW-1	58.0	49.0	1.1	20.1	3.6	14	7.9	580.0	106.0
NW-2	59.0	67.0	1.0	18.5	3.3	21	7.8	775.0	165.0
NW-0	29.0	43.6	0.7	14.5	2.7	5	4.5	175.0	35.0
NW-1	51.6	61.6	1.0	18.0	2.7	3	8.4	524.0	123.9
NW-2	55.4	71.2	1.2	21.3	3.5	6	7.9	619.0	109.9
Soil Series									
Loam	56.6	45.0	0.9	15.7	2.6	12	6.9	407.0	82.5
Adobe	18.0	25.5	0.6	14.5	2.7	3	6.6	92.0	13.6
Sand	7.9	13.9	0.5	7.0	1.7	2	4.9	41.6	6.6
Dune Garden Series									
Main	29.0	43.6	0.7	14.5	2.7	5	4.5	175.0	35.0
Shelter	51.4	58.6	0.9	9.8	1.8	6		100.0	20.3
Ridge	2.0	4.9	0.3	2.2	0.8			0.5	0.1
<u>Godetia grandiflora</u>									
Sun and Shade Series									
%									
100	49.0	54.0	1.3	4.2	1.1	30	6.4	992.0	260.0
60	110.0	46.0	1.4	6.0	1.6	14	6.4	830.0	227.0
35	140.0	38.0	1.1	5.6	1.7	7	6.4	420.0	87.0
20	162.0	37.0	0.7	6.5	1.9	3	6.5	290.0	52.0
10	123.0	14.0	0.4	5.0	1.8	1	4.5	25.0	5.3
100	51.0	46.0	1.3	3.9	0.8	11	5.3	377.0	115.0
60	84.4	50.8	1.0	5.6	1.2	21	5.9	312.0	179.0
35	43.6	22.8	0.3	4.0	1.1	1	4.3	457.0	110.0
20	110.0	22.4	0.4	4.9	1.2	4	4.7	70.0	20.0
10	111.6	45.6	0.8	6.1	1.3	12	5.6	4.5	1.0
5	58.4	8.6	0.3	4.3	1.2	1	4.2	3.6	0.5
Nutrient Series									
NW-0	54.0	32.0	0.9	3.1	0.7	5	4.5	112.0	37.0
NW-1	51.0	46.0	1.3	3.9	0.8	10	5.3	377.0	115.0
NW-2	52.4	54.0	1.7	4.9	1.0	17	6.1	537.0	167.8
Dune Garden Series									
Main	15.4	24.6	0.6	13.1	5.9	3	3.0	35.3	12.0
Shelter	3.9	10.8	0.3	4.9	2.8	0		2.6	0.6
Ridge	2.0	3.6	0.5	2.2	1.3	0		0.2	0.1



TABLE 13 (CONT'D)

Habitat	Plant		Stem	Leaf		Flowers		Weight	
	Height	Width	Diam.	Length	Width	No.	Diam.	Fresh	Dry
	cm	cm	cm	cm	cm		cm	gm	gm
<u>Madia elegans</u>									
Sun and Shade Series									
%									
100	78.0	63.0	1.0	10.0	1.6		4.6	42.6	8.9
10	96.5	32.0	0.3	8.2	1.1		3.9	30.1	4.6
5	74.5	19.1	0.2	6.2	0.8		3.3	12.8	2.5
100	85.0	38.0	1.0	15.9	2.6	16	4.4	300.0	80.0
10	107.0	24.0	0.5	11.4	1.8	2	3.5	55.2	10.2
5	78.0	12.0	0.2	5.5	1.9	3	2.9	7.6	1.4
100	69.0	47.0	1.2	12.6	2.0	16	4.3		
60	129.0	65.0	1.7	15.4	2.7	8	3.3		
35	121.0	61.0	1.5	15.5	2.5	12	3.6		
20	90.0	31.0	0.8	15.1	2.5	Buds			
10	56.0	10.0	0.3	5.2	0.9	1	2.5		
Length of Day Series									
Long-day	62.0	44.8	0.7	10.6	1.1	12	4.5	51.0	13.5
Mid-day	39.0	20.8	0.8	10.6	1.3	5	3.8	137.0	26.5
Short-day	45.4	30.6	1.0	11.4	1.7	5	2.4	28.8	5.4
Nutrient Series									
NW-0	70.0	31.0	1.0	14.9	1.8	11	3.8	68.5	21.6
NW-1	85.0	38.0	1.0	15.9	2.6	16	4.4	110.0	45.5
NW-2	91.0	51.0	1.1	15.3	2.8	15	4.3	253.5	103.0
NW-0	72.9	53.6	0.7	7.8	1.2		4.3	28.7	5.9
NW-1	78.0	63.0	0.9	10.1	1.6		4.6	42.5	8.9
NW-2	75.5	58.1	1.1	10.4	1.7		4.4	88.0	16.2
NW-0	64.0	39.0	1.0	12.5	1.6	4	3.5	133.4	37.6
NW-1	80.0	46.0	1.2	11.3	1.8	13	3.9	287.7	88.7
NW-2	83.0	49.0	1.6	11.4	1.9	20	3.9	746.0	221.5
Dune Garden Series									
Main	62.5	54.9	0.8	7.7	1.2		4.4	23.7	5.3
Shelter	15.2		0.4	6.0	0.6		3.3	4.7	1.4
Main	70.0	31.0	1.0	14.9	1.8	11	3.8	52.6	14.3
Shelter	45.0	25.0	0.7	7.3	1.1	3	3.9	33.0	8.9
Ridge	10.3	3.8	0.2	2.6	0.3	1	2.7	2.5	0.9
Main	64.0	39.0	1.0	12.5	1.6	4	3.5	133.4	37.6
Shelter	14.8	3.5	0.3	3.6	0.4	2	0.9	3.4	1.2
Ridge	15.5	2.2	0.2	2.0	0.2	1	1.5	0.4	0.1
Soil Series									
Loam	83.5	64.5	1.0	9.7	1.9		4.6	129.8	24.9
Adobe	67.5	56.5	0.8	9.0	1.8		4.6	48.9	9.3
Sand	35.6	23.1	0.4	5.4	0.8		3.9	7.9	1.6
Loam	79.8	53.4	1.0	11.1	1.2	25	3.8	71.0	16.2
Adobe	65.2	38.6	0.7	8.6	1.4	12	3.8	50.5	11.5
Sand	28.6	14.2	0.4	6.0	0.5	5	4.0	23.7	6.4
Loam	92.0	47.0	1.0	13.8	2.4	23	4.3	300.0	80.2
Adobe	35.0	16.0	0.4	9.3	0.9	4	4.3	176.0	46.0
Sand	23.0	6.0	0.3	4.3	0.4	2	3.5	4.7	0.8
Loam	82.0	52.0	1.4	10.0	2.9	23	3.6	545.0	127.9
Adobe	65.0	25.0	1.0	10.6	1.5	3	3.3	312.4	94.5
Sand	17.0	5.0	0.3	2.9	0.3	1	1.8	12.7	0.9

SPECIES TABLES  
TABLE 13 (CONT'D)

Habitat	Plant		Stem	Leaf		Flowers		Weight	
	Height cm	Width cm	Diam. cm	Length cm	Width cm	No.	Diam. cm	Fresh gm	Dry gm
<u>Mimulus cardinalis</u>									
Sun and Shade Series									
%									
100	45.8	46.6	0.8	7.1	3.6	20	2.6	152.0	38.2
60	31.2	23.2	0.7	8.3	3.5	3	2.7	44.0	8.6
35	27.6	20.8	0.7	8.9	4.2	7	2.8	26.2	5.1
20	38.0	19.0	0.5	9.3	4.5	2	2.8	16.6	2.8
10	11.9	11.3	0.3	7.7	3.3	0		2.5	0.6
5	22.2	18.2	0.4	9.4	3.9	0		6.3	1.2
Length of Day Series									
Long-day	33.2	31.0	0.8	7.1	3.3	17	2.6	322.0	68.2
Mid-day	16.2	30.8	0.8	7.4	3.4	0		172.0	29.2
Short-day	29.6	36.8	0.8	8.8	4.1	0		125.0	19.2
Long-day	24.0	24.0	0.5	5.3	2.5	2	2.6	50.0	11.9
Mid-day	11.0	11.0	0.5	5.7	2.7	0		64.0	14.0
Short-day	13.0	21.0	0.5	6.3	2.7	0		43.4	6.8
Nutrient Series									
NW-0	18.0	16.0	0.4	5.2	2.4		Buds	31.5	7.8
NW-1	36.0	32.0	0.4	6.5	3.1		"	100.0	23.6
NW-2	46.0	43.0	0.6	7.3	3.9		"	270.0	76.5
NW-0	16.0	20.0	0.5	5.5	2.8	0		45.0	10.0
NW-1	39.0	42.0	0.6	5.9	2.7	11	2.3	115.0	30.0
NW-2	42.0	47.0	0.7	6.2	3.3	13	2.4	165.0	45.0
NW-0	34.8	29.4	0.7	6.1	2.9	6	2.7	54.0	11.7
NW-1	45.8	46.6	0.8	7.1	3.6	20	2.6	152.0	38.2
NW-2	43.8	58.4	0.9	7.0	3.5	29	2.7	232.0	48.5
Soil Series									
Loam	35.0	38.4	0.9	7.8	3.7	14	2.6	156.0	33.7
Adobe	17.7	22.0	0.6	7.0	3.1	2	2.6	83.0	14.4
Sand	2.3	2.9	0.2	1.8	1.0	0		1.0	0.3
Dune Garden Series									
Main	34.8	29.4	0.7	6.1	2.9	6	2.7	54.0	11.7
Shelter	3.1	5.7	0.2	2.5	1.2	0		1.7	0.3
Ridge	2.9	3.9	0.2	2.1	1.1	0		0.7	0.2

TABLE 13 (CONT'D)

Habitat	Plant		Stem Diam. cm	Leaf		Flowers		Weight	
	Height cm	Width cm		Length cm	Width cm	No.	Diam. cm	Fresh gm	Dry gm
<u>Phacelia grandiflora</u>									
Sun and Shade Series									
4									
100	80.0	38.0	1.6	9.1	8.6	18	2.9	172.0	45.0
60	79.0	21.0	1.1	8.2	7.7	2	3.4	240.0	53.0
35	86.0	22.0	1.0	8.8	7.7	2	3.1	165.0	30.6
20	98.0	22.0	0.7	9.3	7.7	8	2.8	192.0	39.2
10	95.0	20.0	0.5	9.4	8.0	3	2.9	37.0	7.0
5	62.0	17.0	0.4	8.1	6.7	0		27.0	3.6
100	79.0	61.0	2.6	7.6	7.2	101	3.4	575.0	136.0
60	103.0	38.0	1.6	11.6	10.3	14	3.0	555.0	106.0
35	115.0	41.0	1.3	10.9	9.8	7	3.1	605.0	102.0
20	138.0	61.0	1.1	13.0	11.4	5	3.0	572.0	95.0
10	109.0	37.0	0.6	9.9	8.4	38	2.9	87.0	12.0
5	81.0	29.0	0.4	7.3	5.2	14	2.4	40.0	5.5
Length of Day Series									
Long-day	58.0	20.0	1.3	6.0	5.4	5	3.1	505.0	108.0
Mid-day	21.0	11.0	0.6	4.3	2.3	1	4.9	215.0	28.0
Short-day	16.0	7.0	0.2	1.6	0.7	1	3.8	92.0	7.2
Nutrient Series									
NW-0	45.0	34.0	1.2	5.1	4.9	18	3.1	195.0	47.0
NW-1	79.0	61.0	2.6	7.6	7.2	101	3.4	575.0	136.0
NW-2	86.0	76.0	2.9	9.3	8.4	133	4.0	1040.0	275.0
Soil Series									
Loam	89.0	27.0	1.5	8.8	8.0	20	3.7	205.0	58.4
Adobe	41.0	13.0	0.7	5.1	4.9	2	3.1	97.3	33.6
Sand	16.0	2.5	0.2	1.5	1.2	1	1.8	21.7	6.5
<u>Phacelia campanularia</u>									
Soil Series									
Loam	20.0	36.0	1.0	4.3	4.3	16	1.9	238.0	46.3
Adobe	23.0	22.6	0.7	3.4	3.1	10	2.1	81.0	17.0
Sand	12.3	14.4	0.6	2.7	2.9	3	1.8	33.0	7.3

SPECIES TABLES  
TABLE 13 (CONT'D)

125

Habitat	Plant		Stem	Leaf		Flowers		Height	
	Height	Width	Diam.	Length	Width	No.	Diam.	Fresh	Dry
	cm	cm	cm	cm	cm		cm	gm	gm
<u>Phacelia wnitlavia</u>									
Sun and Shade Series									
%									
100	48.0	63.0	1.3	5.1	4.8	14	1.9		
60	83.0	44.0	0.6	5.7	4.9	21	2.3		
35	68.0	29.0	0.5	4.7	4.2	8	2.1		
20	63.0	39.0	0.4	5.4	4.9	8	2.1		
Length of Day Series									
Long-day	40.6	55.8	0.9	4.9	5.2	18	2.3	164.5	40.5
Mid-day	27.4	27.6	0.8	5.0	5.1	12	1.9	150.5	25.8
Short-day	28.8	25.0	0.9	5.3	5.1	3	2.0	84.3	15.5
Long-day	39.0	39.0	0.7	4.0	3.4	37	2.4	190.4	38.0
Mid-day	23.0	32.0	0.7	3.7	3.1	10	1.9	187.3	35.2
Short-day	32.0	39.0	0.7	4.4	3.7			171.0	31.9
Nutrient Series									
NW-0	42.0	48.2	0.7	4.4	4.1	17	2.3	94.0	22.0
NW-1	47.0	42.6	0.8	4.1	4.2	16	2.5	177.5	38.5
NW-2	47.4	52.6	0.9	7.8	7.0	12	2.2	219.0	47.8
NW-0	43.0	34.0	0.5	4.5	4.1	15	2.4		
NW-1	56.0	42.0	0.8	7.2	6.8	23	2.7		
NW-2	52.0	45.0	0.8	6.4	6.0	20	2.2		
Soil Series									
Loam	47.0	63.0	0.8	4.7	5.0	15	2.4		
Adobe	23.0	14.0	0.2	2.6	2.1	3	2.0		
Sand	10.0	4.0	0.1	1.3	1.1	1	1.6		
Loam	37.6	44.2	0.8	4.6	5.0	20	2.5	500.0	102.6
Adobe	25.2	24.6	0.6	5.1	4.6	7	2.5	110.5	21.0
Sand	30.8	28.0	0.7	4.5	4.5	7	2.3	41.2	10.5
Dune Garden Series									
Main	30.0	39.0	0.5	2.8	2.5	13	2.1	49.3	11.7
Shelter	25.0	17.0	0.4	3.5	3.5	6	1.9	16.4	3.2
Ridge	12.0	4.0	0.2	2.2	1.6	2	2.4	2.1	0.5

TABLE 13 (CONT'D)

Habitat	Plant Height cm	Width cm	Stem Diam. cm	Leaf Length cm	Width cm	Flowers No.	Diam. cm	Weight Fresh gm	Dry gm
<u>Rudbeckia amplexicaulis</u>									
Sun and Shade Series									
100	74.0	43.6	1.5	15.2	5.3	17	1.5	259.0	71.2
60	125.4	46.8	1.5	18.6	6.9	9	1.6	265.5	63.3
35	149.0	69.0	1.5	21.6	7.3	12	1.4	154.5	34.0
20	148.4	52.8	0.8	18.4	6.9	6	1.4	227.0	34.0
Length of Day Series									
Long-day	87.0	57.0	1.3	14.1	5.0	7	1.8	1110.0	283.7
Mid-day	10.6	31.0		14.7	4.0	0		61.0	12.4
Short-day	8.1	24.0		11.6	3.4	0		38.0	8.0
Nutrient Series									
NW-0	62.0	39.0	1.0	11.7	4.5	0		137.0	32.0
NW-1	87.0	19.0	1.7	15.0	6.2	0		640.0	185.0
NW-2	80.0	70.0	2.0	16.0	7.0	0		1085.0	415.0
NW-0	53.8	24.6	0.7	12.2	4.2	5	1.2	39.0	14.0
NW-1	74.0	43.6	1.5	15.2	5.3	17	1.5	259.0	71.2
NW-2	76.4	60.2	1.7	15.7	5.6	24	1.4	472.0	128.1
Soil Series									
Loam	55.0	33.0	0.7	11.3	5.5	0			
Adobe	34.0	21.0	0.5	10.0	4.0	0			
Sand	9.8	1.5	0.1	1.8	0.8				
Loam	89.4	60.4	1.3	15.9	6.3	15	1.5	501.8	146.0
Adobe	53.6	31.0	1.0	13.6	4.8	5	1.4	146.3	38.0
Sand	17.7	3.6	0.2	4.0	1.3	1	0.6	2.1	0.5
Dune Garden Series									
Main	53.8	24.6	0.7	12.2	4.2	5	1.2	39.0	14.0
Shelter	18.0	6.3	0.4	5.6	2.0	0		4.4	1.0
<u>Raphanus sativus</u>									
Length of Day Series									
Long-day	64.0	54.0	0.9	8.4	6.4	46	1.8	87.5	20.5
Mid-day	13.0	25.0	0.6	8.8	6.2	1	3.3	186.1	42.1
Short-day	9.0	22.0	0.7	10.2	6.0	0		190.0	43.7
<u>Triticum sativum</u>									
Length of Day Series									
Spikelets Awns									
Long-day	96.0	17.0	0.3	18.5	1.0 8.9x1.1	8.0		215.0	66.0
Mid-day	68.0	16.0	0.3	22.0	1.1 9.8x0.8	6.0		217.0	75.0
Short-day	81.0	15.0	0.3	28.4	1.3 7.6x0.8	5.8		165.0	52.0

SPECIES TABLES  
TABLE 13 (CONT'D)

127

Competition in Wild Garden Sowings

<u>Criteria</u>	<u>Open ground</u>	<u>Weed group</u>	<u>Family group</u>	<u>Maximum density</u>
<u>Agoseris heterophylla</u>				
Height	62 cm	29 cm	14 cm	5 cm
Leaf	20 x 1 cm	13 x 1 cm	2.5cm x .3mm	8 x 1.5 mm
Head	5 cm	4 cm	3 cm	1 cm
Ray	16 mm	15 mm	12 mm	5 mm
Involucre				
Rows	3	3	2	1-2
Bract no.	7-8	7-8	5-6	5
Fresh weight	20 gm	10.5 gm	3.3 gm	0.4 gm
<u>Baeria gracilis</u>				
Height	40 cm	17.5 cm	12.5 cm	2.5-7 cm
Leaf	5 cm x 1.5 mm	4 cm x 1 mm	3 cm x .7 mm	4-8 x $\frac{1}{2}$ mm
Head	2 cm	1.6 cm	1 cm	.7 cm
Ray no.	11-13	8-11	7-10	1,4-6
length	7-8 mm	5-6 mm	4-6 mm	1-2 mm
Fresh weight	11 gm	4 gm	.2 gm	.001 gm
<u>Gilia dianthoides</u>				
Height	17.5 cm	22 cm	20 cm	10-12 cm
Stem no.	7	3	1	1
Leaf	8.5 cm x 1 mm	2 cm x 1 mm	2 cm x 1 mm	1 cm x .5 mm
Flower no.	25	6-8	5-7	1
size	2 x 1.3 cm	2 x 1 cm	2 x 1 cm	1.2 x .8 cm
Fresh weight	3.3 gm	1.1 gm	.5 gm	.07 gm
<u>Gilia tricolor</u>				
Height-width	65 x 30 cm	62 x 5 cm	20 cm	8.7 cm
Stem diam.	7 mm	2.5 mm	1 mm	.3-.5 mm
Leaf	10 x 3 cm	8 x 2.5 cm	1 cm x 2 mm	.3 cm x .5 mm
Cluster no.	17	5	1-2	1 flower
Flower	17 cm	15 cm	14 cm	8 cm
Fresh weight	43.5 gm	5 gm	.3 gm	.2 gm
<u>Phacelia tanacetifolia</u>				
Height	105 cm	70 cm	25 cm	13.2 cm
Stem diam.	7-8 mm	2.5 mm	.8 mm	.3-.5 mm
Leaf	25 x 7.5 cm	10 x 5 cm	1.4 x .8 cm	.6 x .3 cm
Cluster no.	10	1	1	2 flowers
size	5 x 6 cm	3.5 x 3.7 cm	1.5 x .6 cm	.8 x .6 gm
Flower	1 cm	1 cm	8 mm	6 mm

TABLE 13 (CONT'D)

## Border Effects in Competition Cultures

Arctotis grandis

<u>Criteria</u>	<u>Corner</u>	<u>Margin</u>	<u>Center</u>
Height	52.5 cm	27.5 cm	25 cm
Stem diam.	12 mm	7 mm	5 mm
Leaf	12-15 x 4-5 cm	7-10 x 3.5 cm	5-7 x 2.5 cm
Head no.	17	9	3
size	5.5 cm	5 cm	4 cm
Disk	17-22 mm	15-18 mm	12-15 mm
Ray no.	23-27	21-26	20-23
dimen.	30-33 x 4 mm	27-32 x 4 mm	25-27 x 3 mm
Involucre	18	16	12
Dry weight	10.8 gm	7.5 gm	2.4 gm

Matthiola incana

Height	65-75 cm	25-30 cm	5-6 cm
Width	45.5-65 cm	8-10 cm	1-2 cm
Stem no.	11-12	1-2	0
Cluster no.	50	3	0
Leaf	12 x 3.7 cm	10 x 1 cm	3.8 x .4 cm
Fresh weight	690 gm	15.2 gm	1.6 gm
Dry weight	315 gm	8.1 gm	0.6 gm

Campanula medium

Height	90 cm	47.5 cm
Stem diam	10 mm	3.3 mm
Flower no.	150	5
size	5 x 6.3 cm	2.5 x 4 cm
Fresh weight	921 gm	21 gm

Godetia amoena

Height	103-127 cm	50-62.5 cm
Width	22-27 cm	3-5 cm
Stem diam.	6-8 mm	1-2 mm
Leaf	6.3 x 1.5 cm	3-3.5 x 2-4 mm
Flower	4.5-6 mm	3.4 mm
Fruit	4-5 cm x 5 mm	3-4 cm x 3.2 mm

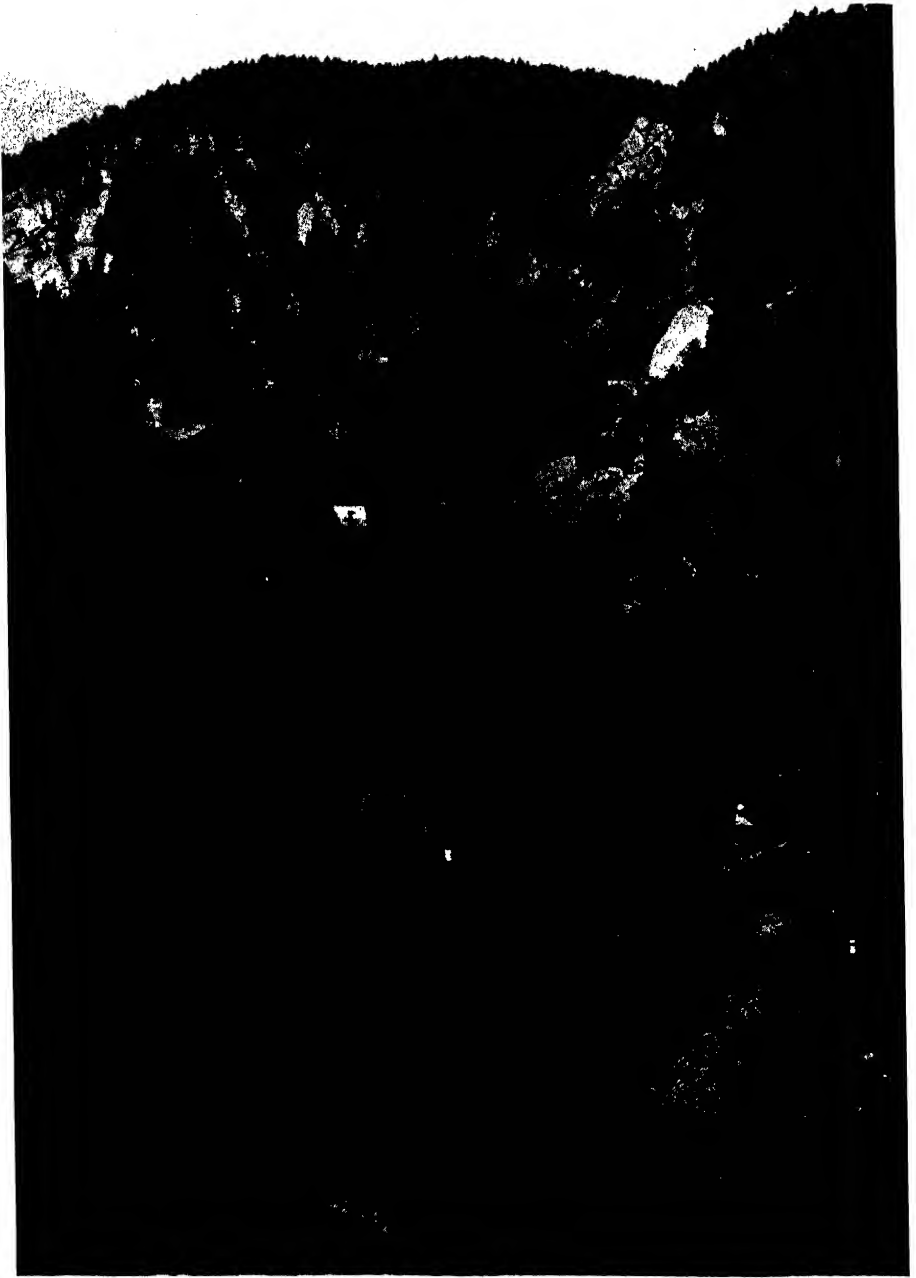
Mentzelia lindleyi

Height	70-87 cm	50-55 cm
Width	60-65 cm	10-20 cm
Stem diam.	8-12 mm	2-4 mm
Leaf		
Flower	5-5.6 cm	2-3 cm

PART II

ALPINE LABORATORY AND  
TRANSPLANT GARDENS





Engelmann Canyon Below Pikes Peak, Colorado.  
Location of the Montane Station of the Alpine Laboratory at 8,000 feet, showing three laboratory buildings in the spruce-fir climax, and greenhouse and gardens next to the Cog Railway.

## II. THE ALPINE LABORATORY AND TRANSPLANT GARDENS

### CHAPTER IV INSTALLATION

**Introduction.**—Ecological studies were begun at the Alpine Laboratory in 1899, a year after the publication of the "Phytogeography of Nebraska" and in extension of the vegetation program laid down there. The exceptional opportunities of the Pikes Peak region for the development of ecology, were first recognized in 1896 in the course of a grazing reconnaissance for the Department of Agriculture. A few of these it shares with all alpine peaks, but most of them are unique. It rises from the plains at 6,000 feet to 14,109 feet, in a distance of seven miles, providing a range of five climates and climaxes equivalent to that from 37° to 67° North latitude. Colorado possesses the greatest area of alpine-subalpine zones on the continent, and its central position has made it the meeting place of northern and southern, eastern and western floras.

The topography is highly dissected, with a number of streams that rise on the Peak and find their way to the plains, thus providing valleys for easy migration upward and downward, and corresponding evolution. These processes have operated upon the five floras represented, but have been most active in the alpine climax, reflecting the conditions supposed to have existed in Holarctica. All this has afforded what is perhaps an unparalleled situation for the study of adaptation and origin in nature, and under control. This has been reinforced by the preservation of natural conditions brought about by the Pike National Forest and the Colorado Springs water reserve. Finally, the Cog Railway has been an invaluable asset in furnishing ready transportation between the several climaxes and gardens and thus conserving time and funds (Plates 38 and 42B).

The repeated upward and downward movement during glacial times, the diversity of topography and soils, and the numerous fragmented habitats, produced much mingling of the original floras, with the widespread evolution of species. This has yielded an exceptionally

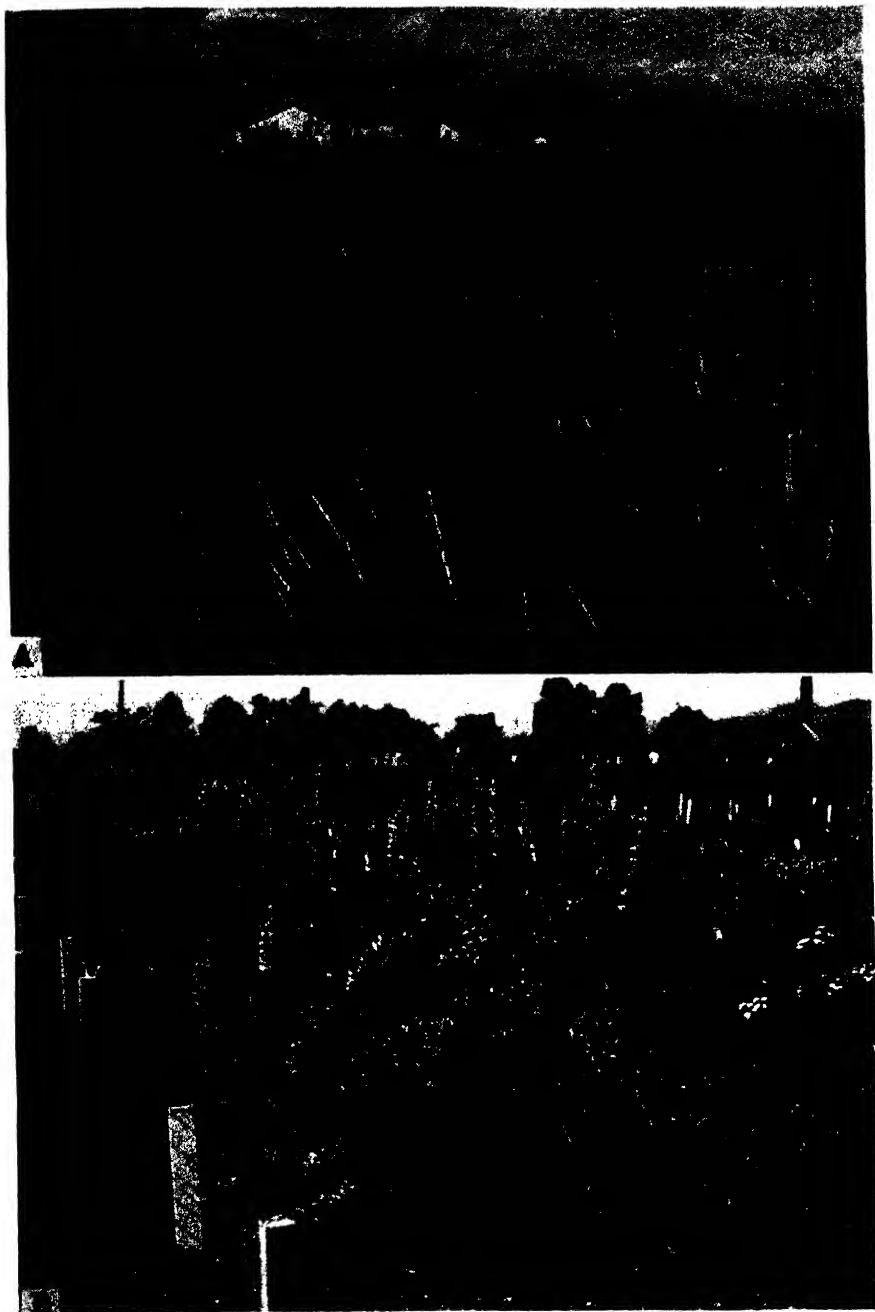
large number of paired species and phylads, or lines of cognate species in which the adaptation to direct physical factors is either evident or suggested. As a consequence, the Alpine Laboratory is probably unsurpassed in the number and variety of natural experiments in origin by adaptation, and hence in the opportunities for re-tracing lines of evolution. This has been accomplished to the degree set forth in the following account, by means of some 18 climatic and edaphic gardens, in which convergence and conversion are constantly at work. In addition, further insight into methods of origin and fixation have been gained by manipulating the food-stream to reveal the manner by which vegetative responses are transmuted into reproductive ones. This has been much favored by the gradual progression of flowering from the lower to the higher limits of the species concerned.

#### TRANSPLANT GARDENS

**General.**—The transplant gardens are all located within an airline distance of 14 miles, from Colorado Springs at 6,000 feet, to the summit of Pikes Peak at 14,109 feet above sea level. Within this distance there is a range of climates from that represented by the mid-grasses, *Stipa* and *Agropyrum* of the Great Plains, to the sparse vegetation of the alpine heights, with the areas between occupied by low-alpine tundra and subalpine and montane forests of spruce, pine and fir.

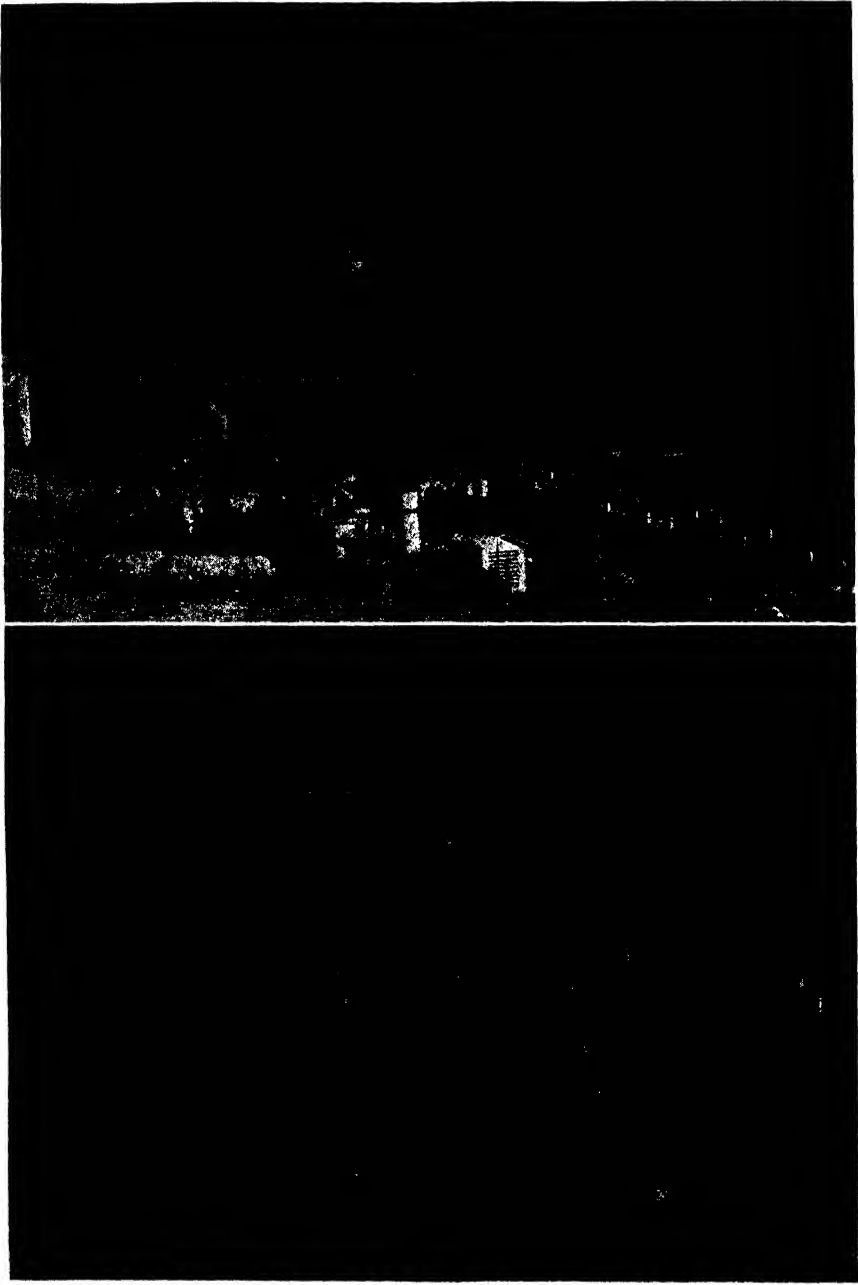
**Plains Station.**—This transplant garden was located at the north-eastern edge of the city of Colorado Springs at an elevation of approximately 6,000 feet above sea-level, and with a mean annual precipitation of about 15 inches. Air temperatures ranged from a mid-winter minimum of a few degrees F. to around 100° F. in summer, the active growing season being about 6 months long (Plate 39).

Most of the transplants in this garden were exposed to the sun, with some in a section where soil moisture was maintained at a relatively high value, and others in plots with comparatively dry soil. Water was available from the Colorado Springs water system. Shade was provided at this station by means of a lath-house, 40' x 60' x 6' high, with standard plaster lath  $1\frac{3}{4}$  inches wide and 4 feet long, spaced approximately  $\frac{1}{2}$  inch apart on all sides and the roof. The light values for this section was 20% of normal sunlight. Another and smaller section was covered with the lath spaced  $\frac{1}{4}$  inch apart which reduced the light to 10% of full sunlight.



Plains Station at 6,000 Feet.

- A. Original climax vegetation of *Stipa viridula*, at the edge of Colorado Springs.  
B. Transplant plots in the Plains Garden nearby.



Gardens at the Montane Station.

- A. Sun-moist Garden in level space between brook and Cog Railway.  
B. Sun-wet Garden in open space near brook with pond and transect beyond.

**Montane Station.**—This station was located in Engelmann Canyon in the montane forest of Douglas fir and Engelmann spruce, at 8,000 feet, the north and south slopes of the canyon providing numerous edaphic habitats of shade and water (Plate 38).

The temperature range from summer to winter is about the same at this station as at the plains, except that the values are a little lower, the maximum approximating 10° F. less. The mean annual precipitation is about 20 inches, with a good deal of it in winter snow, and the active growing season is usually 4 to 5 months long.

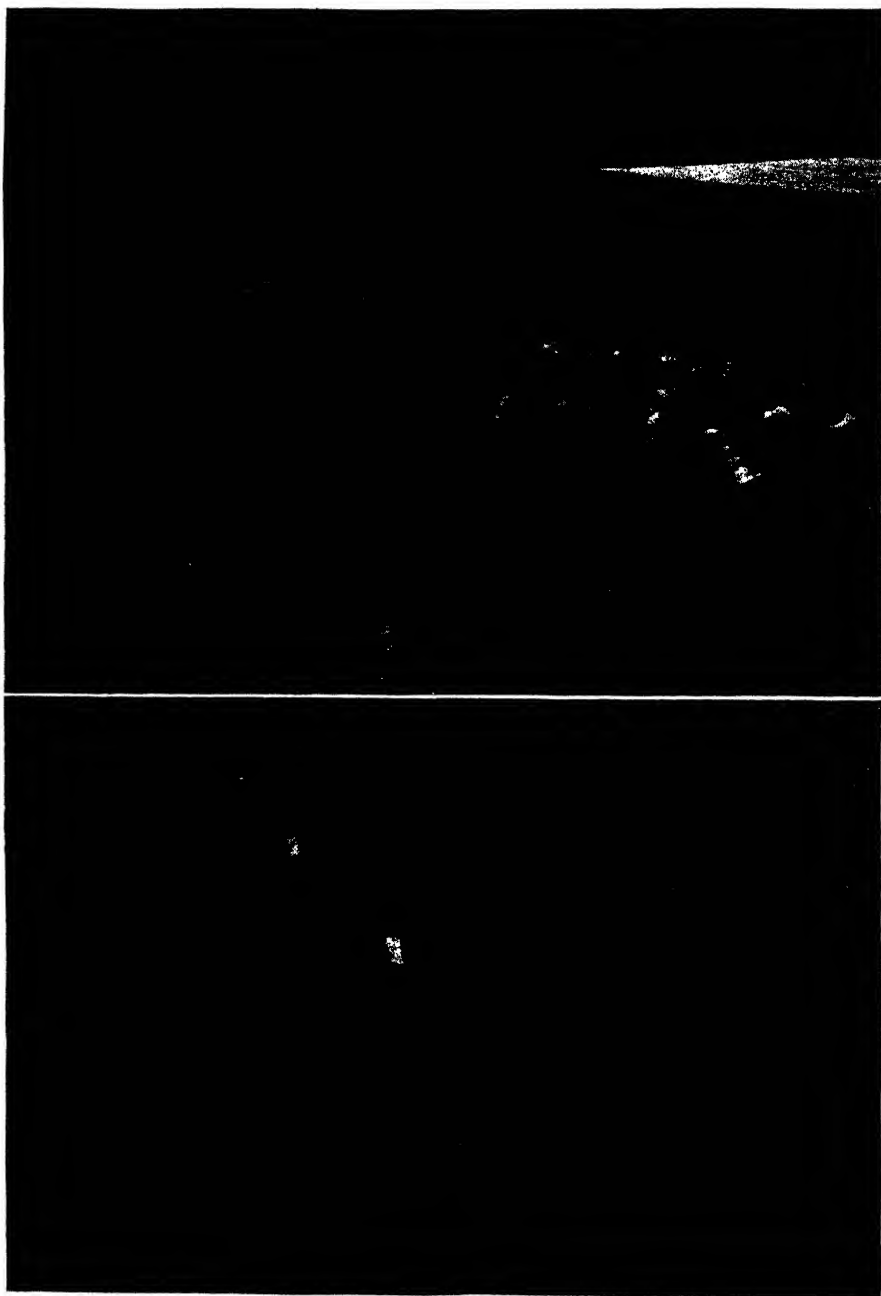
Numerous small gardens were established in the sun and shade of this central location, to produce as many degrees of modification as feasible within a species. The sun-moist and sun-wet gardens were situated in the more level portion of the valley, along the Cog Railroad, while the sun-dry garden occupied a gentle south slope on the opposite side and somewhat further up the grade (Plates 40, 41A). Natural shade was employed for the moist-shade and dry-shade gardens, the former being along the creek in the birch-willow shade, and the latter on the north slope of the canyon wall, in the spruce forest (Plate 41B). Lath-houses, 18' x 20' x 6' high, with lath spaced  $\frac{1}{2}$  inch apart, were used to provide a light-value of 20% without competition from trees.

**Alpine Station.**—This station was located 500 feet above timberline, at an elevation of 12,000 feet, and has a mean annual precipitation of about 25 inches, most of it in the form of snow. The air temperature varies from a midsummer maximum of about 70° F. to a mid-winter minimum well below zero, with the active growing season  $2\frac{1}{2}$  to 3 months long.

Most of the transplants at this station were in the sun, but some were in the shade produced by two lath-houses, each 16' x 32' x 6' high. Three-fourths of the lath-house area was covered by lath spaced  $\frac{1}{2}$  inch apart affording a light value of 20%, and one-fourth by lath spaced  $\frac{1}{4}$  inch apart with 10% of full sunlight (Plate 42A).

Numerous edaphic habitats of water or soil differences were established for the transplants within this region:—

(a). **Nutrients.**—Quadrats were marked out in the climax and subclimax areas for treatment twice each season with an application of Vigoro (Swift & Company organic fertilizer) at the rate of 125 and 250 grams per square meter. Water in addition to rainfall, was sup-



Gardens at the Montane Station.

A. Sun-dry Garden on gentle, south-facing slope.

B. Dry-shade Garden on north-facing slope in spruce forest.

plied to the fertilized quadrats in proportion to the amount of fertilizer added.

(b). **Water.**—A quadrat 1 meter square in the subclimax area was continuously irrigated during the summer season by a stream of water from the water system.

(c). **Competition.**—In one quadrat all the vegetation except forbs, was removed, in another all but the grasses and sedges, and in the control plot all three forms were left. This treatment was applied to the climax and subclimax areas.

(d). **Soil Temperature.**—An enclosed galvanized iron pan, 1 inch thick and 4 feet square, was buried at a depth of 8 inches and parallel to the soil surface. It was made water-tight and connected to a kerosene water-heater which was located in a shelter about 4 feet below the surface of the soil. The water circulated through the pan by gravity and was guided by baffles built in the pan. The soil temperature could be raised 40° to 50° F. easily by this method. A control plot was dug up in the same fashion and the soil replaced on a single sheet of galvanized iron 4 feet square laid at the same depth as the pan.

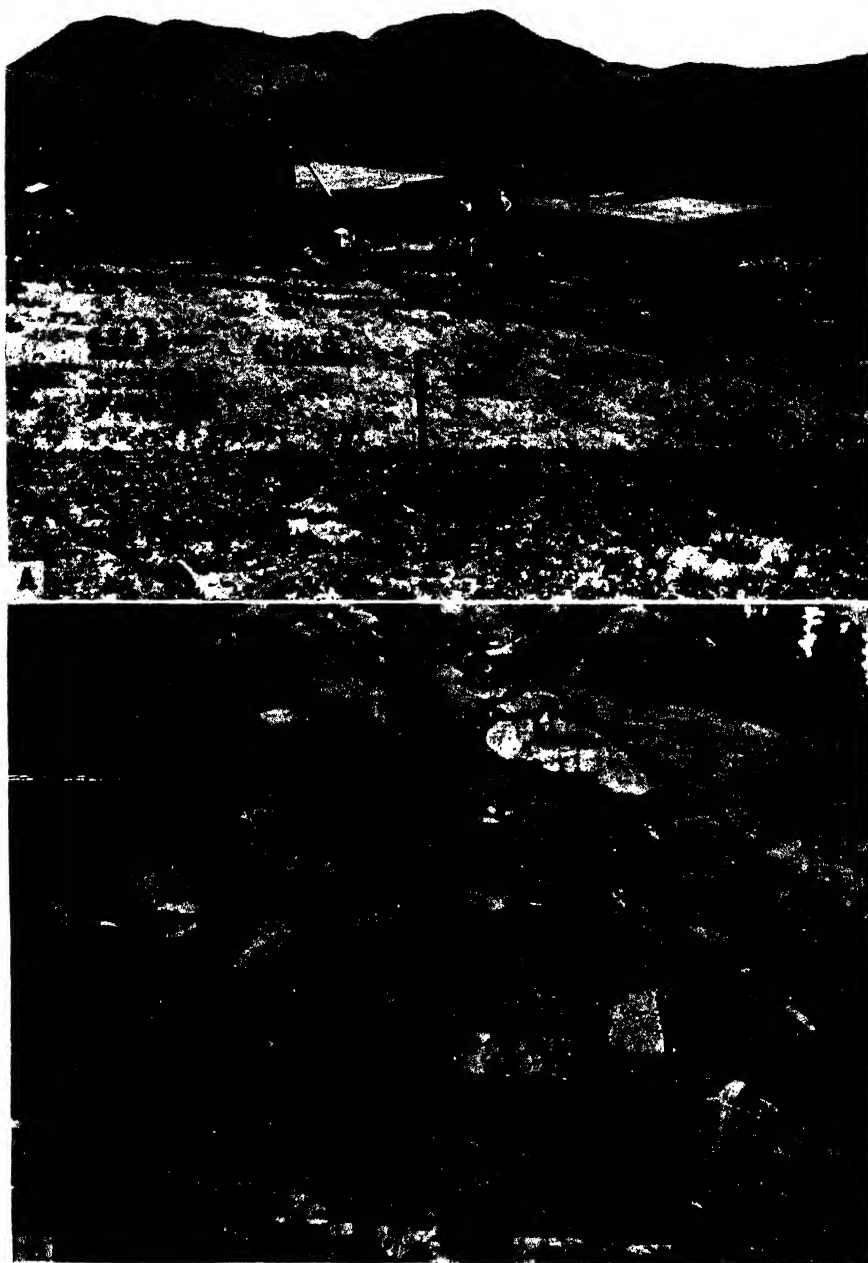
(e). **Soils.**—Four pits 6 feet square and 2 feet deep were filled with the following soils: river sand, adobe, gopher mound soil, and screened climax soil. Twelve native alpine species were transplanted to each of these four pits and have been under observation for five years (Plate 55).

(f). **Reciprocal Sod Transplants.**—A section of sod, 2 feet square and 4 inches thick from each of the climax, subclimax, and gopher mound areas was transferred intact to each of the other two habitats, and have been under observation for seven years.

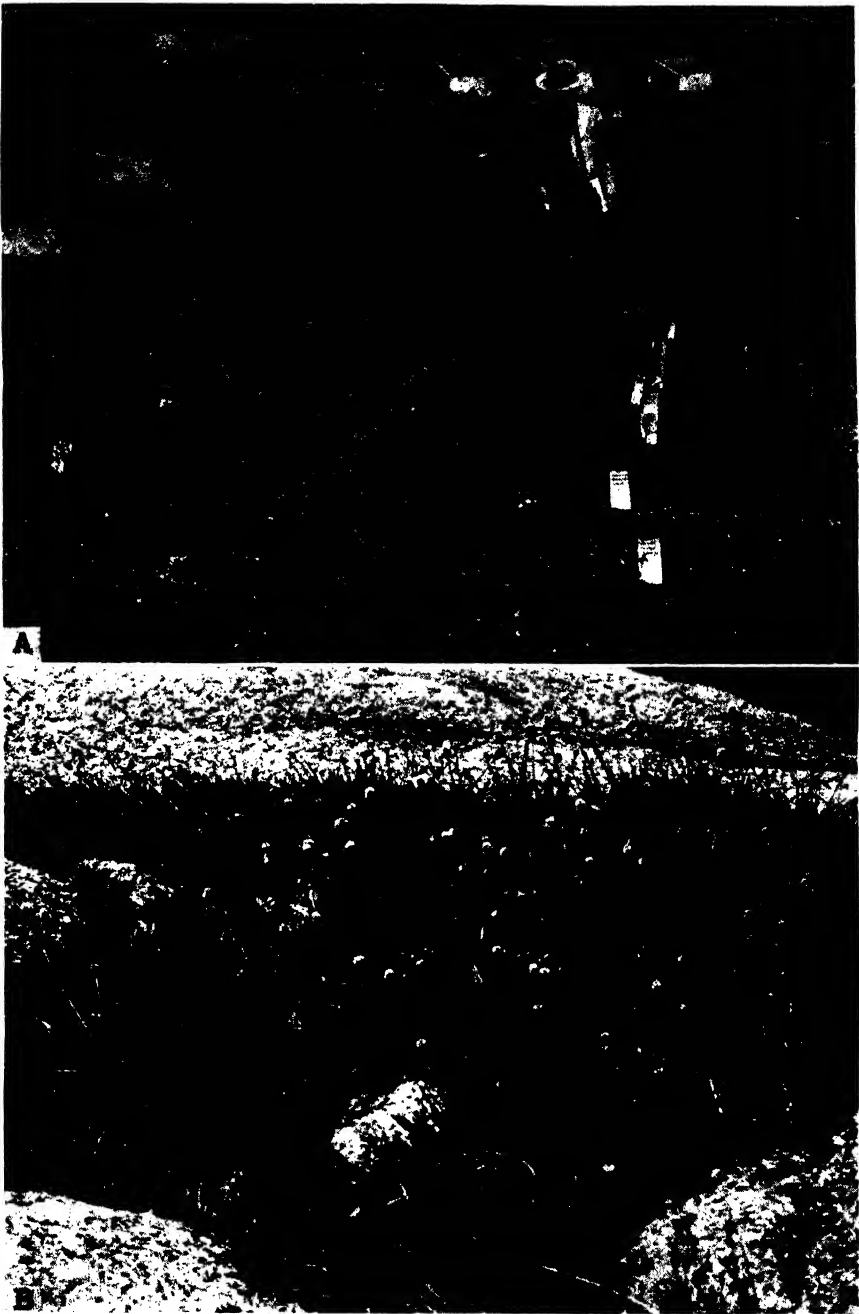
(g). **General.**—In this group, four habitats were concerned: the climax area, subclimax area, slag pile, and below the pool. The slag pile is about 40 feet in diameter and was formed 25 to 50 years ago by the ashes from a coal-burning steam-driven water pump. Certain species thrive around its edge.

An artificial dam was constructed about 50 years ago to impound the water from a spring in the ravine beside the pump-house. The pool formed is about 30 feet in diameter and in consequence, a fair-sized area below the dam is well-watered. A number of native species grow unusually well in this location.





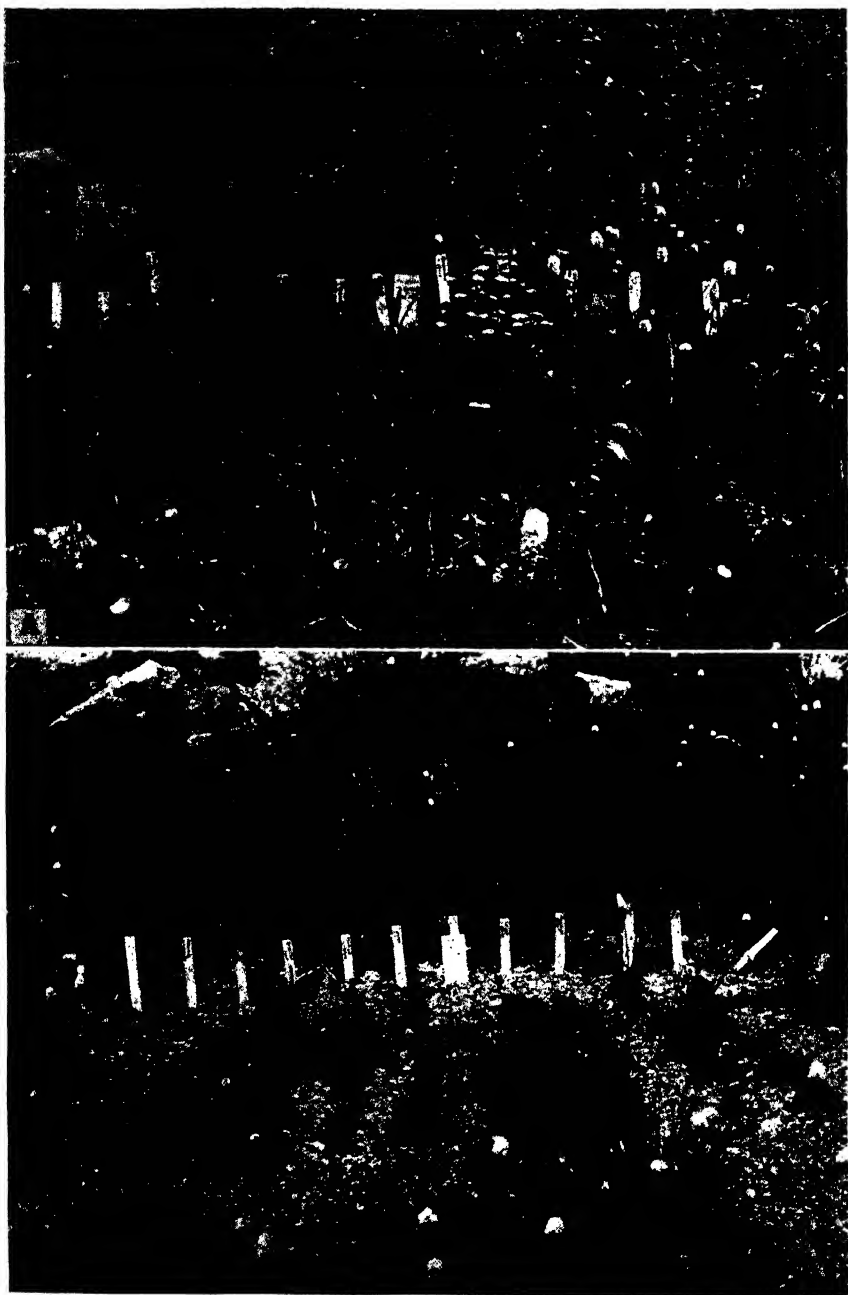
A. Alpine Station at Windy Point on Pikes Peak, 12,000 feet.  
B. Train on Cog Railroad from Manitou to Summit on which transplants were carried between stations.



Alpine Station at 12,000 feet.

A. Transplant plots in the alpine climax.

B. "Gopher-garden," showing luxuriant growth of forbs in the disturbed soil.



Transplant Plots at the Alpine Station.  
A. Edge of slag-pile in the climax.  
B. Ravine below pool, near slag-pile.

Twelve native species taken from the subclimax areas, were transplanted to quadrats about 4 feet square in each of these 4 habitats. These quadrats were cleared of native vegetation at the slag pile and below the pool, but in the climax and subclimax areas, the plants were transplanted with as little disturbance of the native vegetation as possible (Plates 43, 44).

**Mid-alpine Stations.**—A small number of alpine species from 12,000 feet elevation were transplanted to cleared areas at 13,000 and 14,000 feet. These were placed under a complete covering of half-inch mesh hardware cloth for protection against small animals.

#### SEASONAL PHYTOMETERS

**Free Phytometers.**—Plants of the Russian Mammoth variety of *Helianthus annuus* only were used for these series. They were grown in two soil-pits at each of fourteen habitats described above. One soil-pit at each place was made up of the soil native to the habitat, and the other of a sandy loam imported from an area about one-half mile east of the plains garden near Colorado Springs. The latter was surface soil and was richer in humus than the soil native at this garden. The soil-pits in the sun at the plains garden were made 5x7x3 feet deep, while those at the montane station were 4x6x2½ feet deep. The shade pits at the plains and montane stations were 3x4x1½ feet deep, while all pits at the alpine station were 1½x3x1½ feet deep. These sizes were chosen in an attempt to have them large enough to accommodate ten plants each with a minimum of competition, yet not so large that the work involved in constructing them would be prohibitive. The two soil-pits in each habitat were side by side, the native soil being well-spaded and cleared of vegetation.

The field capacities and wilting coefficients of the various soils concerned in this installation are given in table 14. The former were determined by watering the pits well and allowing three days for drainage before sampling. The wilting coefficients were obtained by growing sunflowers in cans holding about two kilograms of soil, and sampling when the plants had wilted. The plains soil is a sandy loam, while the montane soils have a high gravel fraction, except in the shade gardens which have little coarse gravel but considerable humus. The alpine soils are high in gravel with the remainder humus, and have greater field capacities and wilting coefficients than most of the montane soils.

The plants for these pits were obtained as follows: redwood flats, 24 inches square and 6 inches deep, were filled with the imported soil and the surface marked off in 3-inch squares. Three pre-soaked seeds of *Helianthus annuus* were planted in the center of each square, thus allowing some selection for uniformity at the time of transplanting, when they were reduced to one per square. Two weeks after planting the seedlings were removed from the flats and transferred to their places in the pits. This removal was accomplished by means of a square metal tube 3 inches wide on each side and 12 inches long, open on one corner. This device permitted the removal of blocks of soil 3 inches square and 6 inches long, thus practically eliminating disturbance due to transplanting.

The plants were placed in each pit in 2 rows of 5 plants each, spaced as follows: plains sun, rows 26 inches apart and individuals 16 inches apart in the rows; montane sun, 24 inches and 12 inches apart respectively; montane and plains shade pits, 12 inches and 8 inches respectively; all alpine pits, 9 inches and 7 inches respectively. This order was not followed for the alpine pits in 1936, when 2 rows of 6 plants each were employed, the individuals in this case being 6 inches apart in the rows.

All pits except the dry-sun ones were kept watered so that the holard was well above the wilting range. The dry-sun pits were watered only when the plants showed signs of wilting. Water-content samples at depths of 4 and 12 inches in all pits taken each week served as a guide to irrigation requirements. The holard values obtained in 1937 are given in table 15.

In 1936 the seeds were planted on June 24 at the plains garden and grown there until July 7, when the seedlings were transferred to the pits. In 1937 the seeds were sown June 9 and the seedlings were transplanted June 23.

**Sealed Phytometers.**—For the plains and montane stations metal cans 8 inches in diameter and 10 inches tall were used, while for the alpine station cans  $5\frac{1}{2} \times 8$  inches were employed. All had close-fitting lids with a circular hole about 2 inches in diameter at the center. A glass tube extending into a layer of gravel about one inch thick in the bottom of the can permitted the addition of water when needed. All cans of a particular size were given an equal amount of soil and gravel when filled.

In 1936 three pre-soaked seeds of the Russian Mammoth variety of *Helianthus annuus* were planted to each can on June 24. They were allowed to remain at the plains station until July 28, when they were reduced to one per can, the plant nearest in size to the group average being kept. The cans were then sealed around the stem of the plant and taken to their respective habitats. The plains and montane plants were sealed in with sand and cotton, while those at the alpine station had a piece of rubber dam with contact to the stem obtained by using a cellulose glue. Since the plants at this station grew so little, this tight seal caused no apparent damage. Those at the plains and montane stations were protected from rain by canvas covers which were put over the plants only when necessary, while the tight seal used at the alpine station made protection unnecessary. At the first two stations, the cans were placed in a box 3x4 feet and 10½ inches deep sunk in the ground level with the surface, while at the alpine station the boxes were 21x28 inches and 8 inches deep. All boxes were furnished with Celotex covers cut into four strips with notches so that they could be fitted around the stems of the plants. These covers protected the cans from the sun and prevented excessive heating of the soil.

In 1937 a similar set-up was employed except that the cans were filled with a richer soil than in 1936, and one tablespoonful of the commercial fertilizer Vigoro was added to the soil in each can and well mixed with it. This time the openings in the lids were sealed with plastic modelling clay fitted so closely around the stem of the plant that protection against rain was unnecessary. The sealed phytometers at the alpine station had fared so poorly in 1936 that none were installed there the following year. The seeds were planted in the cans at the plains garden June 3 and were moved to their respective places June 28, when they had about 6 leaves each. In both years all stations had 12 plants each at the start. The water-content of the soil was kept as near field capacity as feasible.

#### SHORT-PERIOD PHYTOMETERS

**Standard.**—In both 1936 and 1937 a set of 36 metal cans 6 inches in diameter and 10 inches tall with close-fitting lids were filled with a good loam and planted with three seeds each of the Russian Mammoth variety of *Helianthus annuus*. At the second-leaf stage these were reduced to one plant per can, the one in each can

nearest the group average being retained. As in the case of the seasonal phytometers, the plants were watered by means of a glass tube extending into a layer of gravel in the bottom of the can. Each can was given the same amount of gravel or soil. The plants were grown at the montane station until each had a total leaf surface of from 10 to 15 square decimeters. This much area was needed in order that the plants might have sufficient transpiration to be easily measured for two-hour periods during the daytime. They were then used for periods of one or two days at the various stations and habitats in order to obtain the immediate response to these environments.

The plants were divided into groups with equal average transpiration rates before a series was scheduled, in order to be able to detect small differences in rate in different habitats. With these phytometers standardized in groups of four or six it was possible to measure differences in transpiration rate as small as 5 to 10 per cent with a fairly high degree of certainty. The soil holard was maintained constant within a few per cent both before and during a series. The openings in the lids were sealed with sand and cotton in 1936 and with plastic modelling clay in 1937. Both types reduced evaporation loss to a negligible fraction of the transpiration.

**Native Phytometers.**—These fall naturally into three groups according to the treatment given the plants. (1). A number of individuals of a certain species were taken from the native habitat and transplanted to small cans. They were given several weeks for the root system to overcome injury incurred by transplanting, the first week or two in shade, then they were distributed to various habitats for short-period series of transpiration measurements. (2). These were treated like those under (1) above except that after they had become adjusted following transplanting, all leaves were removed. The plants were then taken to the various habitats where they grew new leaves. After they had again attained a fair size, they were used in short-period series. (3). In these cases, individuals were taken from beds in the transplant gardens, not necessarily their native habitats, transplanted to cans, allowed to become adjusted, and later used in short-period series. These were similar to those under (2) above except that the plants had been grown under different environments a longer time, in some cases several years.

The general procedure in short-period series with groups (2) and (3) was to measure their transpiration over a period of several hours with the plants in the habitats in which they were grown, then bring them all together at the montane station, where they were all run for a series in the shade and one in the sun. This procedure yielded comparative rates of transpiration of the different forms in both sun and shade. After these three series were completed, the leaves were stripped from the plants and their area determined by means of a photoelectric device.

Tables 16, 17, and 18 give general information concerning the native phytometers in the years 1938, 1939, and 1940 respectively. This record includes the source from which the plants were taken, the habitat in which they were grown, the can size, planting date, whether the plants were cut back at time of transplanting, and whether or not new leaves were formed. The date given in some cases after the source is the year in which the plants were transferred from their native habitat to the one given. For a few species in table 5 the planting date is given as 1938, and in these cases the plants had been left over the winter in the lath house at their native station. They were distributed to various habitats as early as possible in 1939. At this time the alpine species were barely coming through the ground, but the montane ones were fairly well-developed.

For all series with these phytometers the soil surface was sealed over with paraffin or beeswax. Between series this seal was partially removed for watering if necessary.



## CHAPTER V

### FACTORS AND CONTROL

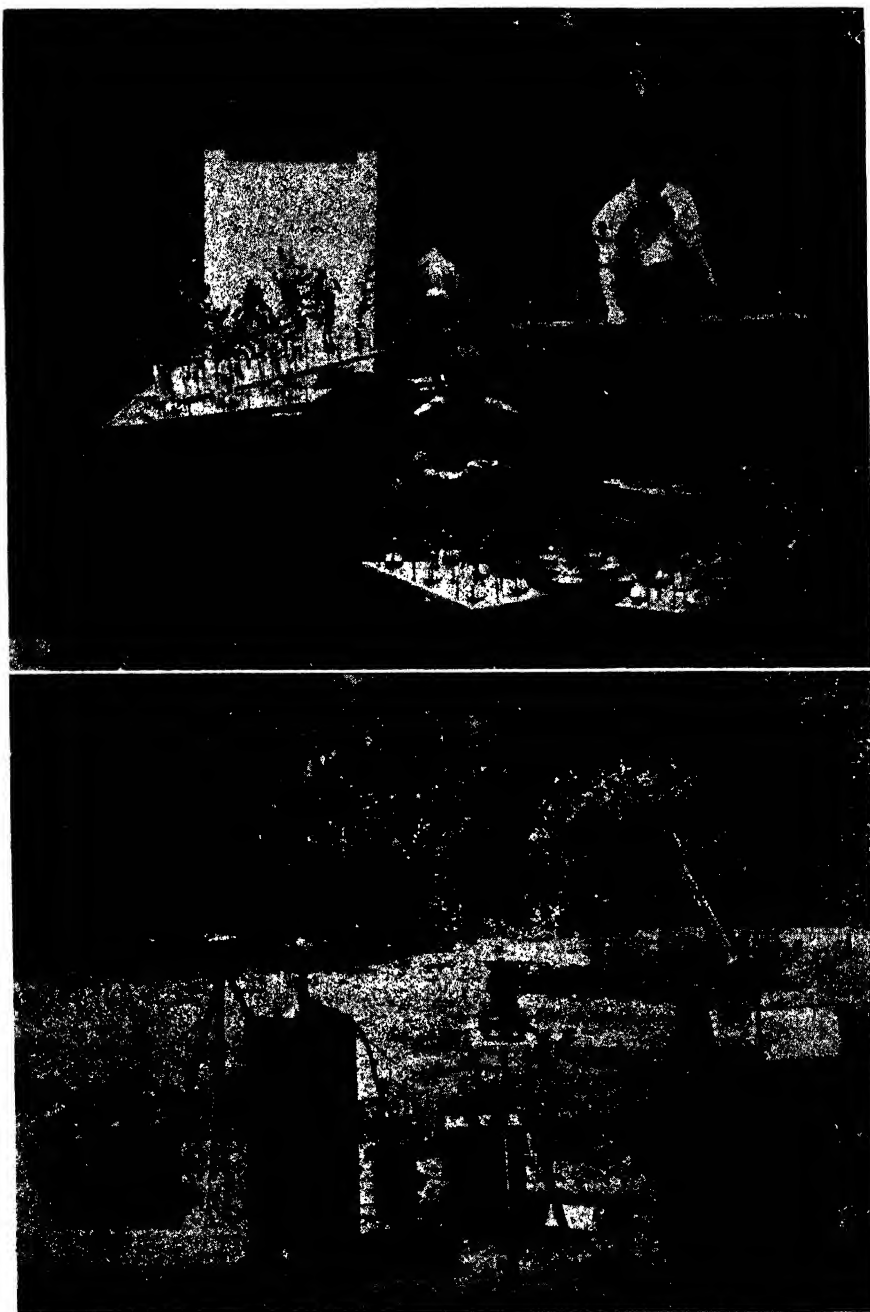
**Methods and Results.**—The battery of recording instruments usually employed at each of the climatic stations consisted of a hygrothermograph, rain gauge, 4-cup anemometer, and white spherical atmometers. The hygrothermograph was enclosed in a white shelter house with louvered sides and placed about six inches above the surface of the ground. The anemometer was mounted with the cups about 18 inches above ground level, and the two white atmometers were mounted at about the same level. In case black atmometers were used, they were mounted about 2 feet from the white ones. All atmometers were outfitted with rain-proofing valves of mercury. All instruments for measurement of factors at the climatic stations were in open places not close to any vegetation which might interfere with the wind movement.

All atmometers were standardized at the beginning and end of the summer season by comparison on a rotating round table in the greenhouse with substandard atmometers referable to Livingston's standard. Soil temperatures were recorded by means of Friez & Sons distance thermographs with an element one inch in diameter and 12 inches long.

Radiation was recorded for two seasons at the montane station and one at the alpine station by means of Eppley pyrhelimeters with photographic recorders. A Smithsonian pyranometer (Abbot & Aldrich, 1916) was available for calibration of the Eppley pyrhelimeters. For protection against hail, the pyrhelimeter at the alpine station was covered continuously with a large arc-shaped piece of  $\frac{1}{3}$  inch mesh hardware cloth, which produced only small ripples in the recorder graph. The pyrhelimeter at the montane station was covered only during hail storms. Radiation in the shade habitats was measured occasionally with a stop-watch photometer (Plate 45).

Black and white atmometers in pairs were used for two seasons at all three climatic stations and in one lath house at the montane station.

Soil moisture samples were taken at intervals by means of a trowel. These samples were restricted to the upper 16 inches of soil. They were



Instrumentation at the Montane Station.  
A. Weighing short-period phytometers.  
B. Pyranometer and Pyrheliometer.

dried in an electric oven at about 100° C. and the results expressed in percentage of the dry weight of the soil.

The seasonal averages of factors at the three main climatic stations for five years are given in table 19, while the weekly averages for the season of 1939 are shown in graphs 13, 14 and 15. In discussing the results, the data from the climatic stations will be presented directly, and the data taken in the various edaphic habitats at a particular station will be discussed in relation to the main climatic factors.

#### PLAINS STATION

**1. Sun Garden** (Plate 39).—This is the main climatic garden at this station, and the data recorded in table 19 were taken in this habitat. Over a period of five years the average air temperature for the season varied from 68° to 70° F., the average daily maximum from 85° to 89°, and the average daily minimum from 51° to 54°. The average relative humidity runs from 50 to 60 per cent, while the average daily minimum is about 20 to 30 per cent. Relative humidity rarely falls below 15 per cent.

For the one season of 1939 a soil thermograph recorded the soil temperature at a depth of four inches. The average was 72° F., with the average daily maximum 86° and the average daily minimum 62° F.

Wind velocity averaged about 3 miles per hour for most of the seasons, with daytime winds of more than 10 miles per hour occurring infrequently.

Rate of evaporation from white spherical atmometers is greatest at this station, as is also the difference between the black and white atmometers. For a period of eight weeks during the season of 1939, this difference averaged 94 milliliters per week.

**2. Lath House.**—Measurements with a stop-watch photometer indicate that the radiation in the section with lath spaced one-half inch apart averages about 20 per cent of the value outside, while that in the section with spacing of one-fourth inch runs about 10 per cent. Air temperatures tend to be slightly lower in the lath houses than outside during the day, but a little higher at night. The 24-hour averages are about the same, the difference rarely being more than 2 or 3 degrees F.

Relative humidity is practically the same inside and out, averaging only a few per cent higher in the lath house. Wind and soil temperature are considerably reduced in the lath house.

## MONTANE STATION

**1. Moist-sun Garden (Plate 40A).**—This garden is located in an open area in the bottom of Englemann canyon and is considered to represent the climatic station in this region. The seasonal average air temperature over the five years shown in table 19 varied from 60° to 65° F., the average daily maximum from 74° to 77°, and the average daily minimum from 45° to 56°.

The average relative humidity varied from 48 to 63 per cent, while the average daily minimum ranged from 23 to 40 per cent. Relative humidity rarely drops below 20 per cent. This station has an average air temperature 7° F. less than the plains sun station, and an average daily maximum 11° less, but an average daily minimum only 2° lower.

Wind velocity is markedly lower than at the plains, being only from one-fourth to one-third as great. This is of course due to protection by canyon walls and the trees.

Evaporation from white atmometers is about 75 to 80 per cent as great as at the plains, while the difference between black and white atmometers for eight weeks in 1939 was only 81 milliliters as compared to 94 at the plains. This indicates a lower total radiation, which is due to the greater cloudiness at the montane station.

Soil temperature at a depth of 4 inches averaged 67° F. for the summer season of 1939, with an average daily maximum of 74° and an average daily minimum of 59°.

**2. Dry-sun Garden (Plate 41A).**—This garden is located about 500 feet farther up Englemann canyon than the sun-moist garden, and is on the south slope near the bottom of the canyon. Thermograph records indicate that the air temperature at this garden runs 1 to 2 degrees F. higher at maximum and about the same amount lower at minimum than in the moist-sun garden.

Relative humidity is slightly lower during the day than in the moist-sun. Soil temperature at a depth of 4 inches runs about 5° F. higher and averages 2° higher. This garden has a little shorter day of sunlight than moist-sun due to shading by rock ridges, the reduction amounting to about 15 minutes both morning and afternoon.

Evaporation from white atmometers averages about 85 per cent of that in moist sun.

**3. Lath Houses (Plates 40A, 41A).**—Three lath houses 20' x 40' x 6' high are located at different places near the canyon floor, all in

sunny locations and all with lath spaced one-half inch apart. Radiation is reduced to about 20 per cent of that outside the houses.

Air temperature runs  $2^{\circ}$  to  $5^{\circ}$  F. lower at maximum and  $1^{\circ}$  to  $3^{\circ}$  higher at minimum than outside, with the averages practically equal. Relative humidity averages about the same inside and out, but is a little higher at minimum inside the lath houses.

Evaporation from white atmometers is about 45 per cent of that outside.

**4. Dry-shade Garden** (Plate 41B).—This garden is located in the spruce shade, up the slope a short distance from the creek. Interception of rainfall by the trees and their competition makes this a fairly dry habitat. Air temperatures are from  $2^{\circ}$  to  $5^{\circ}$  F. lower in this shade area than in the moist-sun garden, both at maximum and at minimum.

Relative humidity is somewhat higher as a consequence of the lower temperatures. Evaporation runs about 45 to 50 per cent of that in the moist-sun garden. Soil temperature averages several degrees lower in the shade. Radiation is exceedingly variable, but averages about 20 per cent.

**5. Wet-shade Garden.**—This garden is located near the brook in an area where the water table is not more than about three feet below the soil surface. Radiation is low here, averaging only about 10 per cent. Air temperatures are only  $1^{\circ}$  to  $2^{\circ}$  lower than in the dry-shade garden, and relative humidity only slightly higher. Evaporation rates are about 5 per cent less than in the dry shade.

**6. Wet-sun Garden** (Plate 40B).—This garden is located on a level area near the brook, and is watered 2 or 3 times per week by means of an irrigating system, the frequency depending upon weather conditions. Air temperatures run slightly lower than in the moist-sun garden. It is shaded by nearby willows and trees, and has about two hours less full sunlight. Evaporation rates are about 60 per cent, and soil temperatures are about  $5^{\circ}$  F. lower. This garden has a layer of imported loam six inches thick to increase the water-holding capacity and fertility of the soil.

#### ALPINE STATION

**1. Climax** (Plate 42A).—This station is located in the general climax vegetation area at an elevation of 12,000 feet above sea level, and about 500 feet above timberline. Over the five-year period for

which data are given in table 19, the air temperature averaged for the summer season between  $46^{\circ}$  and  $49^{\circ}$  F., with an average daily maximum of from  $57^{\circ}$  to  $62^{\circ}$ , and an average daily minimum of from  $37^{\circ}$  to  $40^{\circ}$ . This station has a seasonal average temperature about  $20^{\circ}$  F. less than at the plains garden, an average daily minimum  $14^{\circ}$  less, and an average daily maximum  $26^{\circ}$  lower.

Relative humidity averaged from 57 to 64 per cent, with an average daily minimum of from 35 to 41 per cent. The average daily minimum is only from 10 to 15 per cent greater than at the plains, while the average is only 5 per cent more. In this region, relative humidity rarely falls below 25 per cent.

This station has the highest wind velocities of the three, the mean being about 5 miles per hour. Wind infrequently attains velocities of 15 to 25 miles per hour during the summer season. Trees exposed to the wind show the characteristic distortion.

Rainfall at this station is higher than at either of the other two, and evaporation rates run about 60 per cent of the values at the plains garden. The difference between black and white atmometers averaged 98 milliliters for the season of 1939 as compared to 94 milliliters at the plains.

For the seasons of 1939 and 1940 the Eppley pyrheliometer registered about 15 per cent more total radiation at this station than at the montane. Intensities on a horizontal surface run somewhat higher at this station, the difference being from 10 to 20 per cent on clear days. The maximum intensity on clear days at the montane station runs about 1.5 calories per square centimeter per minute on a horizontal surface, but with the proper configuration of cumulus clouds the value may rise to 2.2. The maximum intensity recorded at the alpine station was  $2.7 \text{ cal/cm}^2/\text{min.}$ , but this value lasted for only a few minutes. On nearly every day the intensity rose above  $2 \text{ cal/cm}^2/\text{min.}$  for short intervals, although the maximum on clear days was usually between 1.6 and 1.8.

Soil temperature at a depth of 4 inches averaged about  $50^{\circ}$  F. at this station, with a diurnal variation of about  $10^{\circ}$ .

**2. Subclimax.**—These areas are interspersed among climax areas over the general landscape in the alpine region; hence no appreciable difference in climate exists.

**3. Gopher Mound** (Plate 43B).—There are numerous mounds in both climax and subclimax areas which have been produced by the burrowing of gophers. These mounds average about 15 feet in diameter and have a rather luxuriant growth of certain forbs. No difference in climate between these areas and the climax has been detected.

**4. Slag Pile** (Plate 44A).—This station is about 2,000 feet from the main climax station and at very nearly the same elevation above sea level. The slag pile is about 40 feet in diameter and 5 feet high at its center. Vegetation grows luxuriantly around its edge, and it was here that the factor data were taken.

Air temperatures run occasionally as much as 5 degrees F. above the climax during the daytime, but with little difference at night. The average is only about 1° to 2° above the climax. Relative humidity is slightly lower during the day at the slag pile, but only a few per cent. Wind velocities are practically equal at the two places.

Evaporation rates average about 10 per cent greater at the slag pile. Soil temperature at 4 inches averages about 5° F. higher at the slag pile due to the dark color of the soil, the difference being greater during the day than at night.

**5. Lath Houses** (Plate 42A).—There are two lath houses, each 32' x 16' x 6' high, for the production of shade at this station. All of one lath house and half of the other are covered with lath spaced one-half inch apart, the remaining portion of the second being covered at a spacing of one-fourth inch. The approximate proportion of radiation in these two sections is 20 per cent and 10 per cent respectively.

Air temperatures run a little lower during the day and a little higher at night, the average being only 1° to 2° less. Relative humidity is a little higher during the day, but the difference is only about 5 per cent. Soil temperature at 4 inches varied from 6° to 10° lower than outside. Wind is reduced to a slight breeze inside the lath house.

Evaporation rates in the half-inch section average about 50 per cent of that in the sun, with that in the fourth-inch section 2 to 3 per cent lower still.

**6. Ravine** (Plate 44B).—This area is about 50 feet from the slag pile, and its bottom is about 10 feet below the surface of the surrounding area. It is immediately below an artificial pool of water formed by

a spring, and consequently is well watered. Air temperatures average only about 2 degrees F. lower than at the nearby slag pile.

Values of holarid in these various edaphic habitats at intervals during the season of 1938 are shown in table 20, and the wilting coefficients and field capacities are given in table 14.

In general the soils at the alpine station have field capacities and wilting coefficients approximately equal to the values for loam at the plains garden. These values range from 15 to 23 per cent in field capacity and from 5 to 7 per cent in wilting coefficient, while at the montane station, the values for the gravelly soils in the sun are about 10 per cent and from 3 to 4 per cent respectively. The soils in the shade at the montane station have more humus than the soils in the sun and consequently higher water-retaining power.



## CHAPTER VI

### FUNCTIONS

#### TRANSPIRATION

**Seasonal Phytometers.**—The results of measurements of transpiration rates of *Helianthus annuus* phytometers for the seasons of 1936 and 1937 are presented in tables 21 and 22 respectively. The data are given as weekly averages of transpiration in grams per plant and in grams per square decimeter of leaf surface per day. Data from the series of 1936 are shown in graph 16. The plants grown at the montane station show a transpiration rate about two-thirds that at the plains, while those at the alpine station run only about half as great. There is very little difference between the lath-houses 20% and 10% at either the plains or alpine stations. The two sun habitats at the montane station are nearly alike in their transpiration rates, while the moist-shade shows a rate about half that in lath-house 20%, with the dry-shade garden intermediate between these two.

At each of the three stations the transpiration rate per unit leaf area in the lath-house 20% is approximately half that in the sun at the same station. However, transpiration in grams per plant shows much greater differences. For example, in 1937 for the week ending July 26, the average transpiration per plant at the plains was 11,009 grams, while in the lath-house 10% the value was only 907 grams, or only about 8 per cent. as great.

The measurements of these sealed phytometers taken at the end of the season are given in table 23, while those from the summer of 1937 are shown in graph 17. The plants are largest at the plains, smallest at the alpine station, with the montane plants intermediate but closer to those at the plains in size. Water requirement values were somewhat erratic, although it seems fairly definite that the plains plants have higher values than those at the montane station, and that those in shade have higher values than those in sun.

#### **Short-period Phytometers.**—

(1). **Climatic Series.**—The results of a two-day series with *Helianthus annuus* on August 13 and 14, 1937, are shown in graph 18.

There were four plants in each location, and weighings were made every two hours. The breaks in the curves are located at the center of the intervals of time between weighings. The habitats concerned in this series were the sun and 20% lath-houses at each of the three stations and the 10% lath-house at the plains and alpine stations. The first day of the series was clear until noon but cloudy most of the afternoon, while the second day was clear except for a short time near noon. Cloudiness was responsible for the dips in the curves. The average transpiration rate at the montane station is about two-thirds or three-fourths that at the plains, while the alpine is only about half the latter. These values agree closely with those obtained from the seasonal phytometers.

At each of the three stations, the transpiration rate in the lath-houses was only about half that in the sun at the same station, and there was little difference between rates in the two lath-houses, although the plants in the 20% section usually had slightly higher rates than those in the 10%.

The reduction in transpiration rate from plains to montane to alpine regions in the sun is to be regarded as due largely to reduced air temperatures and increased relative humidities at the higher altitudes, while that from sun to shade at a particular station is due almost wholly to reduced radiation. The rate at night is low and practically the same in all habitats.

## (2). Edaphic Series.

(a) MONTANE STATION.—The results of a series on Aug. 9, 1937, at the montane station are shown in graph 19. Seven plants were used in each group, and weighings were made every two hours. Values are plotted on the graph at the center of the interval of time between weighings. The transpiration rate at the sun-dry garden was a little higher than in sun-moist, the greatest difference occurring in the morning hours. Plants in both sun gardens averaged about twice the transpiration rate of those in the lath-house 20%, about two and one-half times that in dry-shade, and four times that in moist-shade. The dry-shade garden runs low in the morning hours due to the dense shade of trees, but rises above the lath-house just before noon, owing to increased radiation, and maintains this position most of the afternoon. The moist-shade area has still lower radiation and temperature than the lath-house, and consequently the plants in this location have

only about half the transpiration rate of those in the latter.

(b). ALPINE STATION.—The results of a series on August 26, 1936, are shown in the lower portion of graph 19. Seven plants were used in each group and weighings were made every two hours. The transpiration rate at the slag pile averages a little greater than in the main subclimax areas, probably due to slightly higher air temperatures caused by absorption of radiation by the dark-colored slag. The transpiration rate in the lath-houses is about half that in the sun, with little difference between the lath-houses 20% and 10%. The reduction of transpiration rates in the lath-houses is due largely to reduced radiation and leaf-temperatures, since air temperatures and relative humidities are practically the same inside and out.

**Native Phytometers.**—In table 24 are given data obtained from phytometers of native species in which all plants of a given species were grown under one environment until the start of a short-period series, when the plants were distributed to the various habitats concerned, and weighings were made every two or four hours, depending upon the size of the plants. The results from all species are qualitatively like those obtained from *Helianthus annuus*. At the montane station, the sun-dry plants averaged a little greater transpiration rate than those in sun-moist, with wet-sun lower than either. The lath-house runs 50 to 60 per cent. of the value in sun-moist, with moist-shade and dry-shade about the same or slightly less than the lath-house.

The results from *Geum turbinatum* at the alpine station, and of *Mertensia sibirica* at the montane station, are shown in graph 20. At the alpine station the sun habitats all run about alike in transpiration rate, with the lath-houses from 50 to 80 per cent of the sun values. These native phytometers show greater variation among individuals than *Helianthus annuus* and consequently the average values are not so reliable.

The other type of native phytometer which was used for these experiments, namely the case in which the plants are grown for an extended time in the various habitats concerned before the short-period series was run, gives the response of the plants to their environment after a certain amount of adjustment has taken place, rather than the immediate response given by the former type.

Data obtained from this second type of phytometer are given in tables 25 to 31. The general plan of conducting these series was to

measure the transpiration rates when the plants were in the habitats in which they were grown, then put them all in the shade of the lath-house 20% at the montane station for a few hours, and later place them all in the sun at the montane station. The average transpiration rates are given in the tables, together with the probability according to "Student's" "t" test that the observed differences between sun and shade forms, or between forms from climatically different stations, are accidental.

When the plants are in their native habitats, the sun plants have higher rates than shade species without exception, although in a few cases the difference is not statistically significant. However, when both forms are placed in the same environment, this relation no longer holds. Table 27 gives a summary of the results of this type of comparison for both seasons 1939 and 1940. When both forms are in the shade, their transpiration rates are equal in the vast majority of cases, with relatively few showing differences between the two forms. Of the nine cases in which a difference exists, six have the sun forms with higher rates than the shade plants, while in the other three the opposite is the case.

When the plants are all moved to the sun, there is a definite shift from equality of the two forms toward higher rates in the sun forms, although even in this instance, more than half the cases show equality. Probably the explanation of this behavior lies in the tendency of the shade forms to wilt when exposed to intense radiation, with consequent loss of turgor and reduced rate of water loss.

Stomatal frequency and dimensions, given in table 35, show considerable variation between sun and shade forms. This is also true of dimensions of cuticle, epidermis, and mesophyll given in table 36. In the case of the Canadian variety of *Helianthus annuus*, the sun form at the montane station had approximately three times as many stomata per unit leaf area as the shade form, but still had no greater transpiration rate when placed in the shade. This is probably due to the fact that the sun form had an outer epidermal cell wall approximately twice as thick as the shade form, and consequently had less cuticular transpiration than the latter, although a greater stomatal component. When taken to the sun, the failure of the water supply destroyed the balance between these two components.

Data from plants grown at climatically different stations are given in tables 28 to 31 inclusive. Tables 28 and 29 are for the sun forms,

while 30 and 31 are for the shade forms at the different stations. In general, for the series with the plants in their native habitats, the transpiration rate was greater at the lower elevations. However, there are a few exceptions in which the rates are nearly equal, and a few in which the highest rates were in the alpine region. When the plants were all brought to the montane station for comparison, it was found that little difference existed between the plains and montane forms in most cases whether the comparison was made in sun or shade, while about half the plains and alpine forms were equal. In those cases in which a difference existed between plains and alpine forms, the latter ran highest. With the montane and alpine forms in the sun, about half the species showed the alpine form to have the higher rate, while the remainder were equal.

Of the ten species tested only *Mertensia sibirica* was an exception to the rule that when two climatic forms differed in their transpiration rates, the one from the higher elevation had the greater rate. Even this exception occurred only in the sun, since the two forms concerned, montane and alpine, were equal when placed in the shade. The higher transpiration rates in the higher-altitude forms is probably due to the fact that the leaves of the former are smaller and have a greater number of stomata per unit leaf area, especially in view of the fact that there is relatively little difference in the amount of cutin in the two forms. The internal anatomy of the leaves appears to be affected little by change in elevation above sea-level.

There is also a difference in behavior of the different forms depending upon whether they are in the shade or in the sun. When in shade there are fewer cases in which the difference between the forms is statistically significant than when in the sun. Apparently the alpine forms show a greater response to radiation than the montane ones. This effect may well be due to a greater degree of exposure of leaves to radiation in the smaller forms. A general summary of results of these comparisons is given in tables 32 and 33.

During the season of 1940 seeds of *Helianthus annuus* (S-490) were planted in No. 3 packer's cans each week in sets of ten in order to have each week a group of plants of a given age. Whenever a series was run during this particular summer, a group of these plants was used as a control species in order to have a standard for calculating relative transpiration rates of the various species used as native phytometers. The results are given in table 34. When the plants

were placed in sunlight, none of the species employed had a rate as great as that of *Helianthus annuus*, but when they were in the shade a few were equal to or a little greater than the sunflower. Relative rates in the sun ranged from 21 for *Rubus strigosus* to 95 for *Potentilla gracilis*. The former grows in gravel slides in the sun and is probably as xerophytic a species as any of those investigated. However, *Senecio fendleri* also grows in relatively dry habitats, but its relative position is 75, which is appreciably higher than *Mertensia sibirica* at 50. The latter grows in the sun only in very wet locations. No consistent relation between the relative transpiration rate of a species and the dryness of its habitat is apparent, although a slight correlation seems to exist.

In most cases the relative transpiration rate increased from sun to shade series. Apparently the sunflower responds to radiation to a greater degree than most of the species investigated.

**Detached Shoots and Leaves.**—Shoots or leaves were severed from the plants growing in the gardens, weighed as quickly as possible on a "chainomatic" analytical balance, placed upright in a small jar outside the balance case, and weighed again after a short interval of time. The first weighing usually required no more than one minute, succeeding ones about thirty seconds. Consequently, separate shoots could be weighed each minute, and when only two shoots were being compared, each one could be weighed every two minutes.

Sun and shade forms of several montane species were compared as a check on the results obtained with the short-period phytometers. These comparisons could be made only in the shade, since the leaves wilted quickly in the sun. Another factor limiting comparisons to shade was the fact that considerations of size of leaves usually made it necessary to compare single shade leaves with a sun-shoot having several leaves, thus making an equal exposure to the solar radiation practically impossible.

The values of relative transpiration rates of sun and shade forms are given in table 37. With the single exception of *Rudbeckia hirta*, the sun forms had higher rates than shade forms. The ratio of sun to shade forms for *Rudbeckia hirta* was about 0.5, while in the other species it ranged from 1.03 to 2.25, averaging about 1.5. These results are not entirely in agreement with the short-period phytometers, since in the latter case most species showed equality between the two forms

when both were placed in shade. A reason for this discrepancy is not apparent.

### OSMOTICS

On several occasions during the summers of 1938 and 1939 samples of leaves of numerous species were taken for a determination of the concentration of the expressed sap. The leaves were boiled for about 30 minutes, allowed to cool, and the sap expressed at a pressure of about 4000 pounds per square inch. The temperature depression of the freezing point was determined by means of a Drucker-Burian microthermometer. The concentration of the sap in atmospheres was calculated according to the formula given by Harris and Gortner.

The Ov values obtained are given in tables 38 to 42 inclusive. Tables 38 and 39 give data which probably show the usual diurnal range of Ov values, since one set was taken in midafternoon of a clear warm day and the other the following morning before sunrise. The range in Ov values observed varied from zero to about 3 atmospheres.

The data given in table 40 are probably nearly maximum values of Ov for many of the species at least, since the soil was very dry on that date and many plants were wilting and beginning to shed their leaves. The season was unusually dry, as reference to table 19 will reveal. The moist and wet habitats indicated in the tables were transplant gardens, which were watered, while the dry habitats were native and subject only to rainfall for the water supply. The concentration in several species reached about 20 atmospheres, with the highest at 24.7 for *Solidago humilis* from dry shade. The data taken on this date show the greatest ranges within a species that were observed, the maximum range noted being about 2 in *Senecio cernuus*, *Senecio fendleri*, and *Solidago humilis*. In all three species the largest concentration occurred in dry habitats and was about twice that in moist shade areas.

Tables 41 and 42 give data taken from various habitats at all three main climatic stations. The data show that there is a slight tendency for the concentration to increase with elevation, although in many cases no appreciable difference exists. However, at a given station, Ov values increase regularly with greater dryness of the habitat, whether it is due to atmospheric factors or low holarid. The atmospheric factor data recorded at times of collection of leaf samples are given in table 43.

## GROWTH

**Seasonal Free Phytometers.**—Measurements of the plants at the end of the season are given in tables 44 and 45 for the years 1936 and 1937 respectively. Stem heights and diameters, fresh and dry weights, and leaf areas were determined. Stem heights and dry weights are shown in graph 21.

In presenting and discussing the results, it seems desirable to consider each station separately for response to edaphic factors, leaving the comparison of stations until later.

(a). **Plains Station.**—At this station the only habitats concerned are sun and shade. As usual, the shade plants are very slender compared with sun plants, but with little difference in height. However, there is a great reduction in leaf area, stem diameter, and dry weight in the shade, the ratio of sun to shade dry weights being about 100 in the imported soil series. There is little difference in response in the lath-houses 20% and 10%. The imported soil produces much better plants in the sun, but has little effect in the shade where it is apparent that sufficient minerals and water are available in the native soil for the comparatively poor growth exhibited under the reduced radiation.

(b). **Montane Station.**—The two sun habitats at this station are much alike in their effects on the plants, although the dry-sun produces somewhat better plants, presumably due to the slightly warmer soil. The native soil at the dry-sun garden appears to be more fertile than that in the moist-sun, because the ratio of dry-weights in the native soil varies from 2 to 5, while in the imported soil it is only slightly larger than 1. The somewhat better growth in the imported soil at the dry-sun garden appears to be due to the warmer soil or slightly longer day, while the native soil is likewise more fertile.

The response to shade is similar to that at the plains station, the plants in the lath-house 20% being about the same height as those in the sun or a little taller, but much more slender and having a much lower dry weight. In imported soil, the moist-sun plants have a dry weight from 7 to 14 times as great as those in the lath-house, while for the native soil the ratio lies between 2 and 6. Another of the shade habitats at this station is the dry-shade garden, in which the total radiation is practically the same as in the lath-house, but the plants there are somewhat shorter and have only about half the dry weight of the latter. This is presumably due to the fact that air temperature averages



several degrees lower than in the lath-house. The still further reduction in stature and dry weight for the plants in the moist-shade habitat is evidently due to the greater reduction in radiation.

There is considerable improvement in growth in the imported soil as compared to the native soils at all habitats except the moist-shade, where the plants grew so little that apparently the native soil could supply all the nutrients and water needed. In contrast to the behavior at the plains, the native soil in the lath-house 20% produced only half the dry weight of those in imported soil, while at the plains the two soils acted alike. This is probably due to the fact that the native soil at the plains is much more fertile than that at the montane station. The former is a sandy loam, while the latter has a large gravel fraction.

(c). **Alpine Station.**—As measured by the response of *Helianthus annuus*, the four habitats in the sun at this station seem to be much alike, although the slag pile has a slight advantage, presumably due to the warmer soil. The differences between the other stations are to be regarded as probably not significant.

As at the other two stations, the response to shade is marked. The stem height is about the same or a little greater in the lath-houses than in the sun, stem diameter about half, and dry weight from 20 to 25 per cent as much. The imported soil produces better plants at all sun habitats, the ratio of dry weights varying from 1.5 to 3, but in the shade no improvement was apparent.

(d). **Comparison of Stations.**—Comparing the sun habitats, growth at the plains in imported soil proves to be about three times as great as at the montane station, as measured by dry weight, and from 100 to 200 times as great as at the alpine gardens. The ratios of growth in native soils at the three stations are about 10 for plains to montane and about 20 for plains to alpine. The plants at the montane station have about the same height as those at the plains, but considerably smaller leaf area and stem diameter.

Other interesting comparisons of response to different environments are afforded by the shade plants at the lower altitude stations and the sun plants at the alpine station. For example, in 1936 the dry weight of the plants in the native soil in lath-house 10% at the plains is practically identical with that of those in the imported soil at the slag pile at the alpine station, but the fresh weight is nearly twice as great, stem height is five times, stem diameter a little less, and leaf

area twice as large. The plants in the two habitats were able to produce practically the same final dry weight of material, but the resulting forms of the plants were very different. This is an excellent illustration of the modification in form of plants possible under widely different environments.

In addition to the actual measurements of the plants, it is of value to consider the ratios of height to diameter of the stem and of height to dry weight. These two ratios are given in the last two columns of tables 44 and 45. In 1936 the ratio of height to diameter of the stem in the sun at the plains was about 51 and in the lath-house about 200. At the montane station this ratio varied from 50 to 60 in the sun and was about 140 in the lath-house, while at the alpine station the sun ratios were of the order of 35 and the lath-houses 60 to 70. The values obtained in 1937 were qualitatively like those of 1936.

In the case of ratios of height to dry weight, the span is much greater, increasing from sun to shade and with greater elevation above sea level. The plants in the imported soil at the plains garden had the lowest ratio, 0.67, the lath-house plants at the plains from 30 to 55, the sun plants at the montane station from 1.69 to 5.58 and the shade plants from 23 to 122, while at the alpine station the ratios in the sun ranged from 11 to 23 and in the lath-houses from 53 to 61. These ratios clearly illustrate the difference in form of the plants under different environments.

**Mean Growth Rates.**—In the summer of 1939, plants of *Helianthus annuus* were used for a determination of what we choose to call "mean growth rate," identical with Gregory's "net assimilation rate." It is defined as the increase in dry weight of a plant per unit leaf area over a period of time. The average leaf area may be determined by dividing the difference between the final and initial leaf areas by the difference of their natural logarithms. The increment in dry weight may be determined by the difference in dry weight of two sets of plants, harvested at different times. In the experiments reported in this paper, plants were harvested once each week. In the first series, 8 plants were taken off at the same time, and in the second 25. The final leaf areas, dry weights, and "mean growth rates" from the two series are given in table 46.

At the plains garden the wet-sun plants grew larger than those in sun-dry and had a slightly larger "mean growth rate," the values be-

ing 0.330 and 0.352 for sun-dry and sun-wet respectively for the second series and 0.266 and 0.367 for the first. At the montane station, the sun-wet values are less than the sun-dry in both series, while in the second the sun-moist plants ran highest. This anomalous behavior is probably due to the fact that these sun-wet, sun-dry and sun-moist installations were in different gardens which exhibit considerable differences in soil. All montane values were less than those at the plains. The lowest value observed was in the moist-shade in the second series, a value of 0.053 as compared with the sun-wet value of 0.352, a range of 7 times. Gregory finds that the "mean growth rate" is essentially constant in all environments, but these results do not substantiate his view.

## CHAPTER VII

### ECOGENESIS

Ecogenesis is used as the comprehensive term for the origin of new forms by the ece or environment, and is derived from two familiar Greek roots meaning "born in the house." It is uniquely appropriate for designating all evolution in which the motive force is derived from the environment, and may well prove to include the origin of all new forms, since in the last analysis the chief factors in hybridization—wind, bees and man—must be regarded as ecial factors. While this view has much in common with that of Lamarck and of Waagen and their followers, notably the paleontologists, it differs in its endeavor to harmonize all known processes of change on the sole basis of ecological measurement and experiment. It was first advanced as the result of field and control cultures in *Research Methods in Ecology* (1905) and further elaborated in 1907 and 1908. Since that time it has afforded the basis for an increasingly effective attack upon the problems of evolution in the field, and has led irresistibly to the thesis that all new forms arise out of the environment as the proximate or remote cause, a probability admitted by even the greatest opponents of adaptation, Weisman and DeVries.

It was early discovered that the origin of species did not constitute a definite objective, since the species of manual and monograph proved to be of every possible rank and value, and always without experimental and objective warrant. As a consequence the primary objectives were definitized as the origin of new forms of every degree, fixation, constancy and reversibility. By fixation is understood the accumulation of a new habit or response until it becomes hereditary, while constancy is restricted to the range of variation within the group of individuals. Reversibility is in large measure the corollary of fixation, since it deals with the causes and processes by which a character may be lost or regained. In the experimental analysis, it has been a distinct advantage to keep each objective separate from the others in so far as possible. Thus, origin is not dependent upon fixation, though constancy may be to some extent a measure of the latter. The idea of constancy is helpful in distinguishing between fixed genetic units and

ecads, and is one of the first points to be considered in the experimental analysis of a specific stock. It already appears probable, however, that the prevalent opinion that forms are constant or not constant will have to be modified so that varying degrees of constancy may be recognized.

**Nature of Species.**—As with the genus, there has been much divergence of views as to whether the species is merely a concept or an actual entity. The general opinion is that the species is a concept, but this seems to deal with the term and its application rather than with the unit itself. Once granted that the term might have been applied to any other unit, or an altogether different term used, it seems evident that the unit itself is as definite an entity as the plant community. Like the genus, the species represents a certain portion of the line of evolution, and it lacks definiteness only where evolution has progressed uniformly, without sharp divergences or breaks. Practically all species are still susceptible of modification, and many of them exhibit it most actively. If only the end results of this process are known, as in the case of herbarium studies, they appear to be distinct units, often with little or no evidence of their common origin. As a consequence, units of every possible degree of differentiation and value are masquerading as species in existing taxonomy. As long as species are made in the herbarium instead of the field, this condition must continue, at least in some degree, but it will disappear rapidly before statistical and experimental studies in the natural habitats. Such studies have already reached the point where it is possible to relate a number of recent segregates to their proper specific stock, and they indicate that this will be the regular outcome of such methods.

**The Genetic Definition.**—Many attempts have been made to provide a working definition of the term species, but these have been successful only in leading to widely divergent usages. The old definition based upon sterility has long been discarded, but its place has been taken in some measure by the definition of the geneticists, which is based upon gametic purity. This basis has actually been proposed by Lotsy (1916), and it does have the advantage of being more objective than the other. It is however, of use to geneticists alone, since gametic purity can be determined only by genetic analysis, and this is applicable so far to relatively few cases (1940, 1945). Plants entirely identical in all external characters may exhibit a different gametic composition,

as indicated by their behavior when hybridized, and would accordingly constitute different species. It is obvious that such a definition of the species is impractical, and that genetic analysis can be of value taxonomically only in studying differentiation within the species itself.

**The Evolutionary Definition.**—To the student of evolution, tests of gametic purity, constancy and recognizability, proposed as defining species arise from an incomplete view of the field and suffer from the bias of the specialist. While they all have their meaning, this is as yet too little understood to make them more than interesting working hypotheses. There is no warrant in our present knowledge of the course of evolution for assuming that they have any more connection with the species than with the most recent ecad or mutant. The evolutionary view of the species is that it is a definite phylogenetic stock, sprung from and related to similar stocks, and itself undergoing modification into a number of variads. As they have recently come from the same stock, these variads are more nearly related to each other than they are to those of any other species, and they represent a definite phylogenetic unit, the species, at the same time that they mark its further differentiation. The only definite measure of the progress of evolution is found in the degree of morphological difference, and species necessarily share this basis with other units. To ask that all species show the same degree of morphological difference is to misunderstand the nature of evolution, but it is possible to demand that the great majority of them show a definite difference in the proper position in the sequence of units. In short, a species must not only show adequate morphological differentiation, but this must bear a definite relation to that of the genus on the one hand and of the variads on the other. In an evolutionary taxonomy, therefore, each unit must be determined as much or more by its relation to the unit that precedes and the one that follows as by its purely structural characters.

The inadequacy of a strict morphological basis for species is due chiefly to the paramount role of divergence. If two species have been differentiated from the original stock by the impact of reciprocal factors, such as greater wetness on the one hand and dryness on the other, this very divergence will give opportunity for convergence when they invade reverse habitats. This convergence may sometimes become practical identity (Clements 1904), but as a rule, ancestral or related characters will furnish the clue to descent. Thus, while evolutionary

taxonomy does not pretend to offer a definition of the species, it does provide the method by which species can be recognized and by which they can be related to each other as well as to major and minor units.

### EXPERIMENT

**In Nature.**—Although the exact use of statistical methods in the study of variation and adaptation, affords practical certainty as to the origin and relationship of variads, the actual origin has already occurred, and its nature and causes must be determined by experiment. As a matter of convenience, experiments may be designated as natural and artificial, although the line between them is slight. Natural experiments are those in which various migration agents have carried migrules into adjacent habitats and the individuals have undergone definite adaptation to the controlling factor and become ecads. In cases where the migration is interrupted, the question of descent lacks the final degree of certainty where more than one parent species may be concerned. In mountain regions where the topography is rugged and rapidly changing, habitats are so fragmented that they recur again and again in the same relation to each other. This offers ideal conditions for the invasion of new habitats, and the ecads of plastic species occur repeatedly. In many cases, gravity is the migration agent, and in others the annual extension of rootstock or runner brings about invasion. In both instances there is not only complete continuity in space, but often also in time, so that the question of the specific stock from which the ecad has sprung is as certain as in experiments started artificially.

**Under Control.**—Controlled experiments differ from natural ones chiefly in that the question of origin is always a matter of certainty. They differ also in being carried on necessarily under control, owing to the fact that the number of individuals is limited, and no chances can be taken with their loss. In nature there may be a hundred or a thousand individuals of an ecad in one spot, and this may occur repeatedly in a restricted mountain region, so that protection is rarely necessary. In artificial experiments, control and natural conditions are often antagonistic, and the decision between them must be made upon the basis of the results desired. In the case of hybridization, this difficulty does not exist, since physical factors are not taken into account, and investigations of this process are specially adapted to garden and greenhouse. On the other hand, the origin and differentiation of existing species and ecads can best be studied in the field, since garden and

greenhouse conditions can only be made to approximate natural habitats at the best. However, the plasticity of species and their reaction to known factors furnish admirable subjects for study under complete control, and certain aspects of mutation are also best studied in this manner.

**Methods.**—The primary methods of experiment in the field are transplanting, planting, seeding and modification of the habitat. Transplanting consists of transferring the adult plant from one climate, habitat, or situation to another. It is reciprocal when two related species, a species and its variad, or two related variads are concerned. Climatic transplants are those in which a species is transferred from one climate or subclimate to another or to more than one, as when alpine species are moved to the montane and plains region, or a dominant of the true prairie to the mixed prairie and the bunchgrass prairie. Habitat or edaphic transplants deal primarily with the transfer within the habitats of the same climax, i.e. between the climax and one or more seral habitats, or the latter alone. Planting seedlings from the greenhouse or nursery, or sowing seed under proper precautions, takes advantage of the fact that the seedling is usually more plastic than the adult, but it is subject to many more dangers during ecesis. The modification of the habitat is one of the best methods, chiefly because it permits the modification of a whole group of individuals in position. It is further valuable in furnishing a check upon the behavior of related individuals transplanted to conditions similar to those produced by the modification.

A certain amount of control can be exerted over physical factors in the case of field experiments, such as increasing or diminishing the water-content of an area, or changing the light intensity by clearing or shading, when part of a group or community may be left under the original conditions to serve as a check. In a sense, moreover, a kind of control is assured when plants are transferred from sun to shade or from wet to dry. Garden experiments represent those in the field in the extent to which factors can be controlled or manipulated, and in both, complete measurements of all the major factors are indispensable. In greenhouse and lath-house, the opportunities for control and manipulation are much greater, and studies of adaptation to definite amounts of factor stimuli can be carried on with greater convenience and certainty especially where a sequence of intensities is desired. The meas-



urement of the factors is indispensable here as in the field, in order to permit the correlation of definite quantities of response with equally definite amounts of the controlling factor.

The constant endeavor throughout the long series of experiments has been to render the methods as exhaustive and the attack as complete as possible, in the fullest realization of the fact that much evolutionary effort has been misdirected by reason of a partial viewpoint. No conceivable agent of change has been neglected, from the whole round of physical factors through food, hormones, enzymes, etc. to parasites, animals and man, and both factor and function have been objects of detailed measurement or definite control. Experiments have been carried out consistently in the native habitat and these have been so correlated with the numerous natural experiments in a rugged mountain region as to leave no question of their essential identity. The number of control and induced experiments out-of-doors is large and has yielded a harvest of illuminating results. This has brought about the installation of the comprehensive series of gardens in both California and Colorado, designed to test the entire sequence of agents, methods and processes. These have been designated as climatic or transplant, adaptation and control gardens, the latter divided into factor, mutation, genetic, reversion, and hybridization gardens, the last dealing with the production of hybrids under natural conditions.

A number of publications of the results obtained in these various aspects of the complete problem of adaptation and origin in the plant world, have already appeared. Detailed accounts of acclimatization experiments may be found in "Experimental Vegetation" (1924) and "Plant Competition" (1929). In addition to researches in acclimatization in the Sierra Nevada gardens, a thorough exploration of the part that genetics play in the nature of species has been made by Clausen, Keck and Heise (1940, 1945). The list of publications dealing with the contributory aspects of the adaptation and control gardens at Santa Barbara and in Colorado, appears in the introduction to this book as well as in the bibliography.

In speaking of adaptation, origin, convergence and conversion of species in the following sections, the species of Gray's manual have been the basis for these processes and from the morphologic viewpoint alone. The so-called species of recent segregators are considered as indicated in each instance, as habitat forms or ecads, varieties or variads, mutants, terads, etc. The exhaustive treatment of the subject of

adaptation and origin with especial reference to a system of classification, has been planned for a future publication of which this book presents merely a preliminary presentation of results so far achieved.

### NATURE'S EXPERIMENTS

Ecads proper make up by far the greater number of strikingly different forms found or produced in nature in the course of the researches of four decades, while the related variants and mutants are fewer in number, less marked in departure, and less clearly connected with the efficient factors. However, much evidence has been obtained to show that ecial mutants are produced by direct factors operating through the nutrition stream to the different organs. The difference between variant and mutant in the ecological sense, is little more than one of degree, though it appears that the former is caused by minute factor dosages acting directly. The term hybrid is used in the current sense, while that of hybrid-mutant has proved useful in discriminating between hybrids in the general Mendelian meaning, and those due to a disturbance of the mitotic processes arising out of hybridization.

The topography and natural features of Engelmann Canyon are so varied as to offer an unusually wide range of different habitats within a comparatively limited area. A fairly level stretch of sunny gravel at the bottom of the canyon is hemmed in by steep north and south slopes of strikingly different constitution and vegetation. The southern exposure of the north slope is characterized by gravel slides alternating with thickets of oak chaparral and leading up into scattered pines and spruces at the top of the ridge. In this complex are to be found many degrees of temperature, water-content and light, from warm, sunny gravel to the coolness and moisture of dense shade. Moreover the gradations and extremes of these factors are so closely associated as to make migration between habitats an easy and frequent occurrence, with consequent adaptations and variations in the morphology of the native species (Plate 38).

The opposite slope of the canyon presents an entirely different and even more varied complex of physical factors and natural habitats. The climax spruce forest clothes this northern facing wall of the canyon so densely for the most part, that the branches intercept much of the rainfall, providing areas of dry shade with grassy openings, and less dense shade with moisture, here and there. At the base of the slope, tall shrubs of oak, willow, birch and mountain maple overhang

a stream with rocky or moist banks, while a brook, arising from hidden springs and snow-banks, bisects the forest with a lateral canyon.

Here then are numerous combinations of shade and moisture and extremes of both, so closely associated that there is scarcely a species of this subalpine region that does not occupy two or more different areas, and undergo changes in harmony with them. The physical factors of these natural habitats have been ascertained and correspond closely with those already recorded in the chapter on installation and factors in the transplant gardens, and are similarly referred to as "sun-dry or dry-sun," "sun-wet or wet-sun," dry-shade," etc.

**Montane Ecads.** (Plates 46-52).—Among the more plastic of these species in natural habitats, *Rudbeckia hirta* and *Solidago missouriensis* show morphological adaptations to a number of different combinations of light and water, while *Galium boreale* is similarly responsive to sunny dry or wet locations as well as to degrees of shade and moisture. *Linaria vulgaris* becomes prostrate in open ground, bunchy and dwarfed in dry-sun and tall and slender in wet soil or shade. *Scutellaria resinosa* is also dwarfed and branching in dry soil with slender unbranched ecads in shade. *Clematis alpina* is normally about 6 inches tall on trailing stems in dry forest shade, and only about half that height in dry gravel. On the other hand, where shady brook-banks are available in the forest, the trailing stems clamber on shrubs or seedling spruces to a height of several feet. *Delphinium scopulorum* may grow 6 feet tall on the banks of a brook, and but a few inches in dry soil, while the shade-loving *Aconitum columbianum* stretches up 6 feet or more, whether in the lath-house as a volunteer or shaded by birch or maple overhanging the stream-bank, but becomes greatly reduced in stature in dry-sun.

The sun and shade forms of *Oenothera caespitosa* and *Aquilegia canadensis*, are equally striking, and *Erysimum asperum* and *Oreocarya virgata* respond in the usual way to varying conditions of shade and moisture. *Corydalis aurea* can be found in a wide range of factors which give rise to typical growth forms, from tall, slender, branched plants in the shade. to luxuriant low-growing individuals where sun-

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drouth dwarfs in gravel, to slender shade forms or even semi-climbers in the oak chaparral, but also in the alpine heights and in the transplant gardens. Not only do the plants as a whole show changes in response to the factors of the habitat, but the flowers present a wide range of sizes and shapes also. A most remarkable change in these took place in a dry summer following a wet winter and spring, when the blossoms in the moister situations were much smaller than usual, viz., 15-20 mm. deep and wide, the lobes being one-third as long as the tube. The commoner form in dry places, strongly suggested *uniflora*, the flower being more or less horizontal and narrow: 8 mm. deep by 5 mm. wide, with lobes cut to the middle. A similarly deeply lobed form had a corolla 10 mm. deep and 12 mm. wide, while a third was 12 mm. deep and 20 mm. wide, with narrower reflexed lobes. This closely resembled *parryi* which, like *uniflora*, is a species of xerophytic habitats (Plates 52B, 66, 67).

During the same unusually dry summer, the flowers of *Castilleja miniata* on exposed slopes, were reduced to a length of 2-2½ cm. and had become essentially those of *parviflora*.

**Alpine Ecads.**—Although there is no such diversity of typography and vegetation at 12,000 feet as in the montane region, granite boulders scattered over the tundra, afford micro-habitats of shade and moisture, to which such plants as *Angelica grayi* respond with striking morphological changes. *Sedum roseum* is one of the many alpine species that forsake the dwarfed form when provided with moisture sufficient to allow of greater growth, even though all other factors remain the same (Plate 53).

This effect is even more convincingly illustrated by the modifications shown in a number of species found in the graduated series of water-content, ranging from the edge of a spring-fed pool, up the slopes of the ravines that lead into the pool, to the dry, upper portions of the climax proper. *Mertensia sibirica* furnishes a typical example of the responses to these various degrees of water-content, with water the only variable factor (Plate 54). Comparable adaptations are those shown by *Polygonum bistorta* and *Geum turbinatum*, both in nature and under control at the Alpine Station (Plate 55).



Natural Ecads at the Montane Station.

- A. *Rudbeckia hirta*: 1. Dry shade; 2. Moist shade; 3. Lath-house shade;  
 4. Sun-wet; 5. Sun-moist; 6. Sun-dry; 7. Competition dwarf.  
 B. *Solidago missouriensis*: 1. Dry gravel; 2. Competition dwarf; 3. Dry gar-  
 den soil; 4. Sun-wet; 5. Normal sun; 6. Bush form; 7. Half shade.



Natural Ecads of *Galium boreale* at 8,000 feet.

- A. 1. Sun-dry; 2. 25% shade in aspen woodland; 3. 20% shade in Lath-house;  
4. Deep shade of forest.
- B. 1. Dry soil; 2. Moist soil; 3. Wet soil; 4. Shade.



Natural Ecads at 8,000 feet.

- A. *Linaria vulgaris*: 1. Prostrate form in open ground; 2. Competition form in dry, sunny spots; 3. Sun-moist Garden; 4. Sun-wet near pool; 5. Shade of willow.
- B. *Scutellaria resinosa*: 1. Drouth dwarf; 2. Dry gravel; 3. Shade of shrub.



Natural Ecads at 8,000 feet.

- A. *Clematis alpina*: 1. Climber in moist deep shade; 2. Dry shade in spruce forest; 3. Dry, sunny gravel.  
 B. *Delphinium scopulorum*: 1. Sun-moist; 2. Sun-dry.  
 C. *Aconitum columbianum*: 1. Volunteer in lath-house shade; 2. Shady brook-bank; 3. Sun-dry.

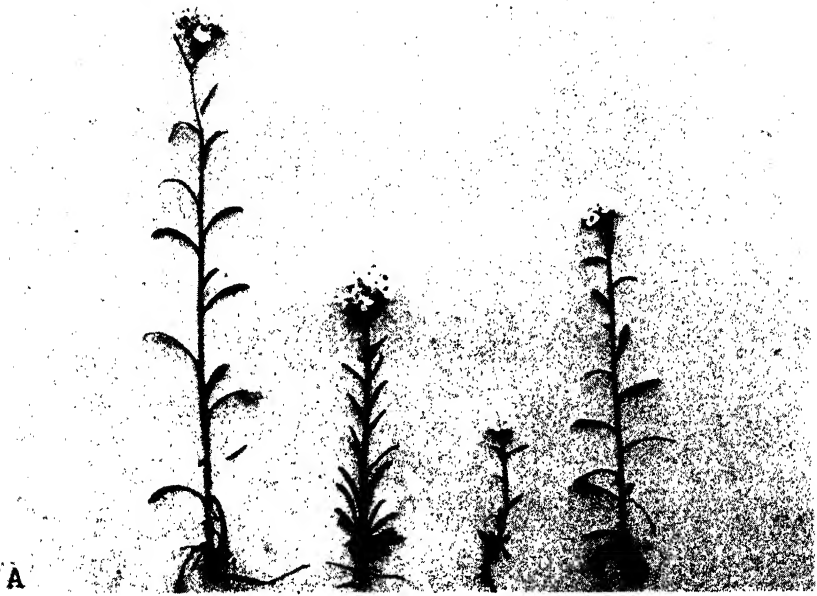


PLATE 50



Natural Ecads at 8,000 feet.

- A. *Oenothera caespitosa*: 1. Normal gravel form; 2. Stemmed form in shade.  
B. *Aquilegia canadensis*: 1. Sun-dry, 10 inches tall; 2. 20% shade, 30 inches tall.



Natural Ecads at the Montane Station.

- A. *Erysimum asperum*: 1. Sun-moist; 2. Normal sun-form; 3. Dry gravel dwarf;  
4. Half-shade.
- B. *Oreocarya virgata*: 1. Dry half-shade; 2. Sun-moist, no competition;  
3. Open aspen shade in moist gravel; 4 & 5: Hard gravel.



Natural Ecads at the Montane Station.

- A. *Corydalis aurea*: 1. Deep shade; 2. Sun-moist; 3. Sun-dry.  
 B. *Campanula rotundifolia*: 1. Dry gravel,  $3\frac{1}{2}$ -6 inches tall; 2. Sun-intermediate, 18 inches; 3. Sun-moist, 23-30 inches; 4. Semi-climbing in shade, 32-38 inches tall.



A.

B.

Natural Ecads at 12,000 feet.

A. *Sedum roseum*: 1. Sun-moist; 2. Sun-dry.

B. *Angelica grayi*: 1. Moist and partly shady rock-cleft; 2. Sun-medium;  
3. Climax dwarf.



A. Ravine in tundra of the Alpine Station, 12,000 feet.  
B. Natural ecads of *Mertensia sibirica*, from moist soil at bottom of ravine to drier soil up the slope in a graduated series of water-content.



Ecads at the Alpine Station, 12,000 feet.

A. *Polygonum bistorta*: 1. Pool; 2. Climax pit of soil; 3. Clay; 4. Sand;  
5. Subclimax; 6. Climax: sun-dry.

B. *Geum turbinatum*: 1. Pool; 2. Lath-house (20%); 3. Edge of gravel-flow;  
4 & 5. Subclimax; 6. Climax.

## CHAPTER VIII

### CONTROLLED EXPERIMENTS

#### METHODS AND OBJECTIVES

The primary objective of the studies in adaptation is the production of new forms under measured control and the relation of these to the ecads resulting from natural experiments. This involves a minute analysis of the process and especially of the extent to which it acts as a selective agent. Consequently it demands not only the detailed correlation of factor and function, but likewise an inquiry into the energy relations concerned in the latter. With respect to evolution, the crux of the problem lies in the reciprocal action of adaptation and fixation and in a comprehensive analysis of heritable and non-heritable changes.

**Gardens.**—Natural and climatic or altitude gardens remain indispensable to interpretation and correlation, but they yield new forms slowly and in small number. Even more serious is their discontinuity, with the consequent doubt as to the role of selection. This is obviated by the use of transects and sequences, especially when they run the entire gamut between wet and dry, or sun to dense shade. These are little more than variations of the same method, the transect being continuous and the sequence interrupted, the one adapted to the gradual change of holard from the center of a pond, the other to the more irregular grouping of light densities in a forest. However, the best transects are those artificially produced to yield a continuous gradient from the submerged ece to dry soil with the lowest chesard that permits growth. A score or more of species may be planted side by side in such transect rows, with both rows and individuals spaced to reduce or eliminate the effects of competition. This affords not only a complete series of ecads, but also furnishes a graphic summary of response from one extreme through the optimum to the other extreme. A phytometer row is included in each transect to provide a standard to which the various species can be referred and to permit the readier investigation of functional responses. Further checks are obtained by growing each species in the control garden, with and without competition and with a modicum of cultivation, to secure definite norms for the climate concerned.

**Transplants.**—Much attention has been devoted to securing decisive evidence of direct adaptation to the habitat as contrasted with an independent selective effect. This is accomplished in the first instance by a tenfold increase in the number of transplants, as well as by the division of mats and rosettes especially, in which each individual yields a large number of clones. In the second instance, autogamy has been utilized to provide seeds of known parentage, artificial selfing proving much more successful than natural, as would be expected. In all cases the uniformity of the response within the species, the harmony between species, correlation with the efficient factor, and agreement with natural ecads furnish further evidence of distinct value.

The mortality due to transplanting has been almost eliminated by improvements in method, as well as by the use of seedlings and other stages, such as rosettes. Of the first importance have been various measures taken to reduce transpiration and the loss of rootlets, and to hasten the regeneration of laterals. These have comprised enlarging the core of earth, watering and covering during digging and transport, and keeping the cores wet and cool for a day or two, followed by several days or more in cool moist shade to promote establishment. This also permits taking advantage of rainy or cloudy days for the final transfer, as well as having a compact core for actual planting. The transplant beds are then shaded and watered until establishment has become certain. A further advantage accrues from the reduction of shock and the fact that the plants undergo more or less normal modification the first season.

**Factors.**—The factors of the habitat are measured in the major stations by means of a complete battery of recording instruments for light, humidity, temperature and wind, with simple instruments for water-content, evaporation, etc. The phytometer is indispensable for evaluating such factors as light, water and temperature in relation to growth, stomatal behavior, transpiration, photosynthesis and respiration (Clements and Goldsmith, 1924). It also furnishes standard or duplicate plants under varying degrees of control for the measurement of functions in the habitat as a requisite for the interpretation of the adaptations produced.

**Exsiccati & Photographs.**—A consistent endeavor has been made to render the system of vouchers and records as complete and accurate





Conversions of *Mertensia lanceolata* and *pratensis*.

- A. *Mertensia lanceolata* to *pratensis*: 1. Normal *lanceolata* in sun; 2. Conversion-form in lath-house shade; 3. *M. pratensis* control in shade.
- B. *Mertensia pratensis* to *lanceolata*: 1. Normal *pratensis* in shade; 2. Conversion-form in sun; 3. *M. lanceolata* control in sun.

as possible. The original group or area is designated, and two or three specimens are selected to serve as vouchers. These are first photographed by means of a naturalist's camera and are then pressed and dried. A group of ten controls is also transferred to the main garden in the climate concerned, to constitute a living record of the stock employed and at the same time make it possible to evaluate the effect of competition. Whenever feasible, the natural ecads are obtained at the same time, photographed with the transplant vouchers and likewise made into exsiccati. Similar vouchers are obtained year by year as the transplants are modified in the respective habitats and these are photographed with replicate vouchers of the originals when the flowering periods overlap. A similar procedure is followed when the modified transplants are returned to their original homes.

**Records.**—The written record is based upon a comprehensive system of numbering, which articulates transplant with control, voucher, photograph and record-card. Each garden has its diagram that shows the position, number of plants of each species, their condition, etc., and is recharted year by year. Each species-group has a label stake that bears the name and number, while each clone is wired with a numbered wooden label. A method of numbering has been devised which indicates at a glance the year, source, destination, habitat, group or parent of each transplant, and is readily carried in mind. It also permits fairly unlimited expansion as the project develops, since the numbers are thus similar for each species. In addition to such mechanical methods as aids in the actual work of transplanting, the results of changes that take place in both natural and controlled experiments are carefully observed and recorded each season. These consist of accurate measurements of all parts of the plant, notes on number and branching of stems, number, size and characteristics of leaves, kind of inflorescence, number and size of flowers, etc. Many of these data appear in the tables reproduced in this book and the complete records are available for reference or further use.

#### SUN AND SHADE TRANSPLANTS

**Reciprocals.**—Reciprocal planting is based upon the presence of paired species, or a species and its ecad in neighboring habitats. At the outset, each transplant was placed in the spot from which its reciprocal was taken, but such sites often proved to be not typical, and the lack of protection in most cases, rendered mortality high. Com-



Adaptations of *Mertensia sibirica*

- A. Transplant ecads: 1. Sun-wet; 2. Sun-moist; 3. 20% shade in lath-house;  
4. Cold, wet soil of brook-bank.
- B. Conversion of *sibirica* to *paniculata*: 1. Typical *sibirica* from brook-bank  
shade; 2. Conversion form; 3. Normal *paniculata*.

petition played a part in this, and constant care was required to prevent invasion by the native controls. The later practice was to treat reciprocals like other phylads with larger numbers and an endeavor was made to install the cultures under fairly extreme conditions for each species.

In the semi-control gardens where the water-content is kept more or less at an optimum, modification is frequent, and in the lath-houses almost universal. This may result merely in the production of shade types conforming closely to the various light intensities or it may lead to conversion, either into a striking new form, into reciprocal intermediates between the two contiguous species, or of one of these into the other, to the extent at least of the morphological criteria concerned.

As a consequence of fire at the Alpine Laboratory in 1917, the herbaceous layer of the Douglas-fir forest was exposed to the sunlight. This led to the modification of the subdominants into sun-forms, closely approaching adjacent forms commonly regarded as species in some cases, and in others producing a new and characteristic sun-form. Chief among the former were *Mertensia pratensis*, the shade species, modified into a form approaching the sun-loving *lanceolata*. This convergence later resulted in actual conversion as a transplant in the alpine sun-garden. After four years exposure to a light intensity of 12% in the lath-house at the Montane Gardens, all the individuals of *lanceolata* have been converted into plants morphologically indistinguishable from the controls of *pratensis*. The reciprocal change was less complete, though most of the sun-plants of *pratensis* closely approximate *lanceolata* and some are essentially identical. Similar success has attended the transplanting of these two species from the Montane to the Alpine Station, where *lanceolata* has been morphologically converted to *pratensis* in the lath-house, and *pratensis* to *lanceolata* in the alpine sun-garden. On the other hand, while a number of striking forms have been produced from the basic *sibirica* and the extreme *alpina*, conversion has proved a more difficult task. Apart from certain fluctuations or "small species" within itself, *sibirica* has been brought close to *pratensis* and *virginica*, and some individuals in the sun-garden have been altered into forms little if at all distinct from *paniculata*, and convergence towards *lanceolata* is marked. Even the extreme species *alpina* has been brought to approximate *lanceolata* closely, and the reciprocal conversion is likewise possible (Frontispiece; Plates 56, 57).



Conversion of sun and shade *Erigerons* at the Montane Station.

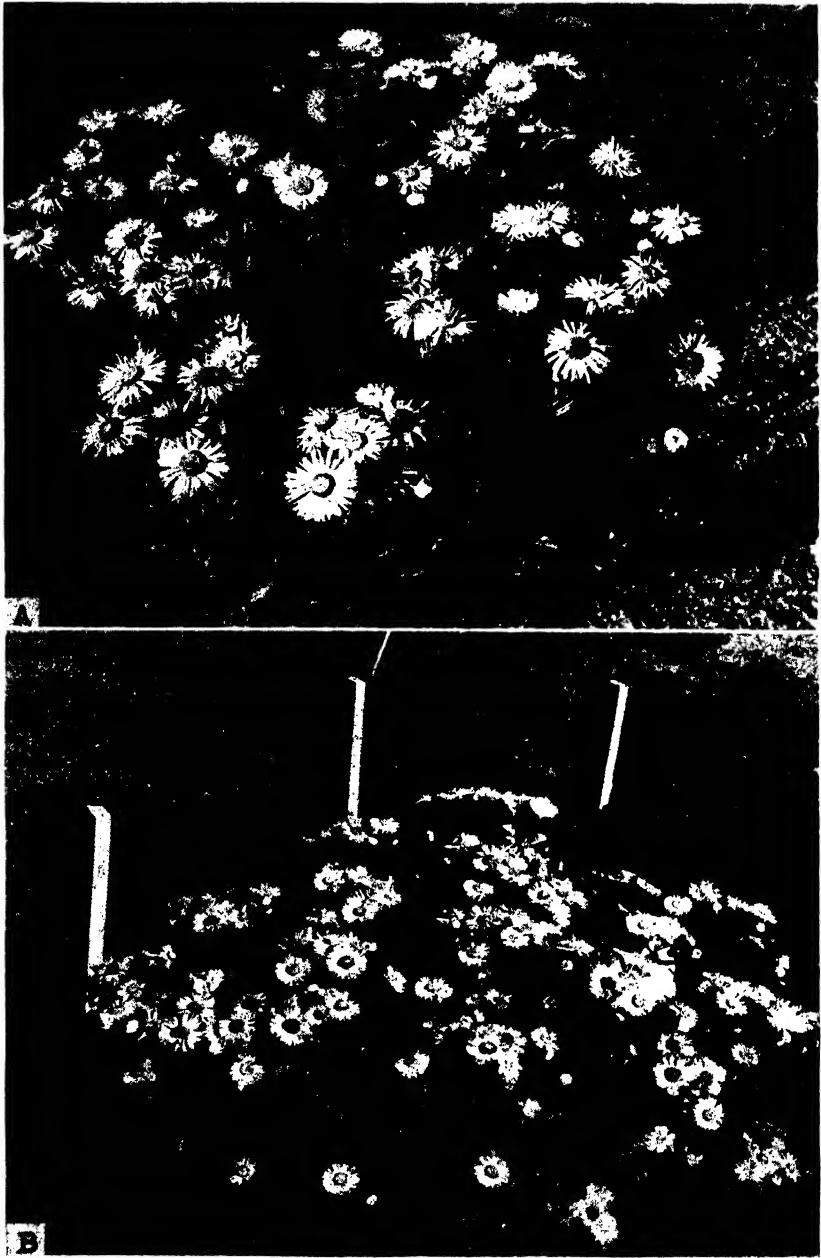
- A. *Erigeron glabellus*: 1. Dry-shade; 2. Moist-shade; 3. Sun-moist which resembles 4. *E. macranthus*, sun-moist.
- B. *Erigeron macranthus* converted to *glabellus* by shade. 1. Normal *macranthus* in dry-sun; 2. Conversion-form; 3. Normal *glabellus* in shade.

Other striking changes following the removal of the forest canopy by fire, occurred with *Erigeron glabellus*. This is a shade species of *Erigeron* with a sun-form, *macranthus*, nearby in the Montane Station. Not only did the exposure to sunlight change *glabellus* to resemble *macranthus*, in a comparatively short period, but eight years later, the plants of *glabellus* that had been placed in the sun-garden at the Plains Station, appeared completely identical with *macranthus* (Plates 58, 59).

The sun-form of *Smilacina stellata* has glaucous leaves which are folded longitudinally and make a sharp angle with the stem. In the shade form, the leaves are flat, horizontally spreading and not glaucous. These are characters that have been used in taxonomic keys for the separation of supposedly distinct species. However, after plants of the sun-form have been grown in moist shady places for a single season, the leaves are identical with those of the shade-form. Conversely, when transplants are taken from the shade and placed in open sunny spots, the leaves become glaucous, tend to fold longitudinally and assume an ascending position. These results have been checked by removing the leafy canopy above plants of the shade-form without changing the rootstocks, when the change to the sun-form becomes complete. Herbarium specimens of the leafy shoots were taken when the transplants were made, or before the canopy was removed, and again from the same rootstocks after the change had occurred. These specimens serve for direct comparison and furnish a definite record of the changes produced (Plate 60).

A complete series of responses to light has been obtained with two apparent varieties of *Rosa acicularis*, namely, *engelmanni* and *sayi*, growing respectively in moist fir forests and in dry gravel. These were transplanted into reciprocal habitats in 1919, and both forms were also transferred to sun, half-shade and full-shade gardens in 1924. In the shade gardens, they had become practically indistinguishable by 1926, and closely similar in the sun. Transplants of *sayi* have changed slowly in moderate shade, but those of *engelmanni* are identical in size, habit, leaves and prickles with neighboring *sayi*. Changes in fruit have occurred also, subglobose growing in the same cluster with ovoid and elliptic ones (Plate 61A).

The behavior of species grown in extreme conditions in the montane zone is exemplified by that of *Senecio fendleri*. The shade ecad grows 30-32 inches tall in contrast to 10-12 in the normal form, and but 2-3 inches when low-holard is combined with sunshine. The stem



Conversion of Sun and Shade *Erigerons* at the Plains Station.

A. *Erigeron glabellus* transplanted from spruce shade at 8,000 feet and grown for eight years in the sun at 6,000 feet, has become indistinguishable from:-

B. *Erigeron macranthus*, also growing in the Plains Garden at 6,000 feet.

of the drouth ecad is densely white-tomentose, and of the others loosely tomentose and green. The leaves of the shade-form are nearly three times as long as broad as those of the normal, and these are twice as long as in the xerad. The clusters of the first are racemose and leafy-bracted, of the second corymbiform and bractless, and of the third, 1-2-headed, the heads being half as large as the others (Plate 61B).

With rare exceptions, shade-forms that are moved into less dense shade or into sun, blossomed more abundantly, while sun-forms transferred to the successive shade gardens, flowered much less or not at all. As a rule, annuals have been found to be more or less readily changeable, perennials more slowly. Stature, branching, leaf-form, inflorescence, time of blooming and number and size of flower and fruit can be modified almost at will by direct manipulation of a particular factor (Plate 62).

#### WATER-CONTENT TRANSPLANTS

A pool for effecting the widest range of adaptation to water, has been constructed at the Montane Station. This permits a series of decreasing holard from submerged and floating through amphibious and saturated, to xerophytic, the land values being approximately 30%, 15%, 7% and 3%. The soil is the same throughout. The water is led from a mountain brook and is much colder than in the ponds and lakes of the plains, thus also permitting transplants between the two, with the temperature difference controlling. The most important forbs, grasses and sedges of the montane zone, especially those with a hydrophytic tendency have been planted in the 5-stage transects from the amphibious zone to dry land, in order to determine the limits of ecesis as well as adaptation to the water and air-contents (Plate 40B).

On the intake side, the entering brooklet has spread over the coarse gravel soil to form a swamp, almost glacial in temperature, in which hydroid mesophytes in particular have been planted. *Epilobium angustifolium* made a remarkable response to the cold saturated soil during the first summer. The stature decreased from 4-6 feet to 8 inches, the leaves from 6-9 by  $\frac{1}{2}$ -1 inch, to 2-3 by 1-1.3 inches, and the raceme from 1-2 feet with 25-75 flowers, to 2-3 inches with 5-6 flowers, while the petals are distinctly larger and the bracts leaf-like. The technical characters of the style alone separate the new form from *latifolium*. Even these had disappeared in a neighboring xeroid dwarf





A



B

Sun and Shade Reciprocals of *Smilacina stellata*.

A. Plains Garden at 6,000 feet: 1. Sun; 2. Shade.

B. Montane Gardens at 8,000 feet: 1. Dry gravel; 2. Sun-moist; 3. Lath-house shade (20%); 4. Moist shade in spruce forest.



Sun and Shade Transplants at 8,000 feet.

A. *Rosa engelmannii*, upper row; *Rosa sayi*, lower row: 1. Dry sun; 2. Moist sun; 3. & 4. Moist shade; 5. Dry shade.

B. *Senecio fendleri*: 1. Full sunlight; 2. Full shade; 3. Drouth dwarf.

of *angustifolium* in which the base of the style was nearly or quite glabrous and the stamens as long as, or longer than, the style.

Under intense competition in 2 inches of water, the stems and leaves of *Typha angustifolia* were decreased to a third the usual size and the pistillate inflorescence vanished completely in those individuals most suppressed. Transplants of the paired species, *Geranium caespitosum* which is xerophytic, and the mesophytic *richardsoni*, have resulted in a few seasons in changing practically all the characters reciprocally, the cut of the leaf proving the most stable.

#### ALTITUDE TRANSPLANTS

**Factors in Alpine Dwarfing.**—Bonnier was the first to make a careful study of alpine plants with respect to the effect of altitude. His final conclusions (1895) were that the characteristic dwarfing and accompanying structural changes were caused primarily by greater light intensity, aided by drier air and lower temperatures. It is important to note that Bonnier, although he made experimental plantings of alpine and lowland plants, gave little or no attention to measuring the factors concerned. As a consequence of his work, the opinion has become general among botanists that light is the chief factor in alpine dwarfing.

**Water.**—When the ecological studies in Colorado were begun in 1899, an attempt was made to explain the behavior of alpine plants upon the basis of Bonnier's conclusions. This proved to be unexpectedly difficult. A number of polydemics of the alpine region were found to be dwarfed in certain habitats, but not in others. *Bistorta*, *Gentiana*, *Potentilla*, *Sedum*, *Sieversia* and others, appeared as dwarfs in habitats with a holard of 5-8 percent, but they grew normally in those with 25-50 percent of water. Frequently the dwarf and normal form may be found within a few feet of each other, where a gravel area touches a tiny pool or rill. Such facts made it evident that the intensity of alpine light was not responsible for dwarfing, since the light-value was necessarily the same for both. In the case of certain species such as *Gentiana amarella*, *Campanula rotundifolia*, etc. dwarf forms occur at 8,000 feet which are in no way distinguishable from those found at 12,000 feet. Moreover, the oaks, which are so characteristic of the foothills, grow as tall at 8,000 feet as they do at 6,000 feet. At both altitudes they are 8-12 feet high along streams, and 1-3 feet in dry places.



Sun and Shade Ecads at 8,000 feet.

A. *Solidago nemoralis*: 1. Lath-house shade (20%), 36 inches tall; 2. Sun, 24 inches tall.

B. *Solidago rigida*: Shade effect of competition: 1. 22 inch specimen in plot of 5; 2. 27 inch plant from plot of 10.

C. *Solidago speciosa*: 1. Sun-moist Garden; 2. Shade-moist Garden.

D. *Galium boreale*: 1. Plant from sun-gravel, 13 inches tall; 2. Plant from aspen shade, 29 inches tall.

**Light.**—Most cases of dwarfing thus seemed to be due to water-content differences and not to intense light. It was imperative, however, to supplement the evidence furnished by the plant, by actual determinations of the light intensity at different altitudes. An exhaustive study of this factor has been made throughout the years, by means of precision instruments for that purpose, such as have already been discussed in preceding chapters. The results obtained have led to the conclusion that there is no appreciable increase in the intensity of the light from 6,000 to 12,000 feet of altitude, and nothing at all of an efficient increase. Taking the intensity at the lowest station as 1, the ratios are 1:1:1 through the middle to the highest station, where it varied occasionally to 1.1 or 1.2 at the most.

**Temperature.**—As soon as it was recognized that light had little to do with alpine dwarfing, it became necessary to look for an efficient cause among the other physical factors. The effect of temperature, especially in connection with shortness of season, was clearly recognized in the beginning when thermograph instruments were installed as early as 1903, at the three stations, and a continuous temperature record from June to the middle of September obtained for four successive seasons. From these, the average temperatures were found to be 10 degrees less at 8,000 feet than at 6,000 feet, and 15-17 degrees less at 12,000 feet than at 8,000. Later more exhaustive studies and records corroborate these earlier findings (Graph 13).

**Length of Season.**—Differences in the length of season are as striking. The season at the Plains Station (6,000 feet) is  $4\frac{1}{2}$ -5 months long; at the Montane Station (8,000 feet), it is  $3\frac{1}{2}$ -4 months, and at the Alpine Station (12,000 feet), scarcely more than  $2\frac{1}{2}$ -3 months, making a difference of approximately  $2\frac{1}{2}$  months between 6,000 and 12,000 feet in altitude. It is evident, therefore, that temperature, which is so intimately connected with growth, and length of season which determines how long growth is possible, must play a large, and perhaps the leading part, in such alpine dwarfing as is not due to water-content differences.

**Humidity and Transpiration.**—Continuous records of humidity were also started in 1905 by means of psychographs and psychrometers, and have been made and extended by other means through the succeeding years. Detailed results appear in the graphs whence the general conclusion seems to indicate that evaporation and transpiration

are considerably lower at the Alpine Station, in spite of the fact that the relative humidity was only 7-10 percent greater than at the Montane Gardens. These results would seem to eliminate humidity as a factor in alpine dwarfing. The chief reason for reduced temperature and evaporation rates at high elevations is, of course, the lower temperatures of the evaporating surfaces in these regions.

#### TRANSPLANTS FROM HIGHER TO LOWER ALTITUDES

Many of the phylad and reciprocal species have been grown for a number of years in the series of climatic gardens, new lots being added each year or two to measure the rate of adaptation, and conversely the original fixity of character. The most important ones have also been installed in the edaphic series for light and for water in order to determine the complete range of adaptation to these factors, as an aid in the interpretation of the results obtained in the phylad gardens generally.

In the transplant gardens special attention has been paid to the question of alpine dwarfs, which are regarded by the ecologist as ecads and by the geneticists at least as ecotypes, the essential difference being that of fixity or heredity. The evidence so far secured suggests that these are not two wholly separate units, but that the one passes into the other as the particular habitat continues to operate. Most alpine species brought down to plains or sea-coast lose the dwarf habit year by year, although the change may be effected in a single year by reducing the light intensity, increasing the soil-water or adding fertilizer. However, transplanting plains or montane species to the alpine climax results in the production of dwarfs the second season in practically all cases, though this effect too may be largely or wholly inhibited by shading, watering or fertilizing.

One of the most constant of alpine dwarfs is *Silene acaulis*. Transferring it to lower altitudes in the sun, has resulted in little or no change, but after several years in the shade, the leaves have elongated more than five times the normal length, and the stem has likewise lengthened and become branched (Plate 63A.B). For five years after transplanting, *Castilleja occidentalis* underwent little modification, but during the following three, it steadily approached *pallida* from which it has apparently sprung. In the same period, *Gentiana frigida* has stretched up in the shade to several times the height of the alpine dwarf, and has developed leafy nodes, with a terminal cyme of three



A



B



C

Transplants from Higher to Lower Altitudes.

- A. *Silene acaulis*: Field Portrait of alpine native at 12,000 feet.  
 B. *Silene acaulis*: 1. Alpine dwarf; 2. Transplant in shade at 8,000 feet;  
 3. Ecad produced by 5 years of shade at 8,000 feet.  
 C. *Gentiana frigida*: 1. Native alpine dwarf; 2, 3, and 4. Stages in adaptation  
 to 5 years of deep shade at 8,000 feet.

flowers and lateral ones below (Plate 63C). *Luzula spicata* has elongated gradually from year to year, and the breaking up of the compound spike into a racemose arrangement of stalked spikes, finally occurred.

Although some characters are easily modified, others prove much less plastic. This applies even to such variables as stature, at least when it is coupled with other characters. The alpine variety of *Solidago humilus*, for example, retains the depressed habit during its first growing season after being transplanted from 12,000 to 8,000 feet, where its reciprocal attains a stature of 1-3 feet. Similarly, *Zygadenus alpinus* continues dwarfed and produces flowers when only 2-3 inches high, even when grown alongside its reciprocal, typical *elegans*, which is 1-2 feet tall. However, each year the evidence increases to show that adaptation is a cumulative process with many species, especially those at first regarded as stable perennials. With annuals and plastic perennials, pronounced changes may occur in the course of a few years under sufficiently extreme conditions.

The alpine *Agropyrum scribneri*, for instance, after being transplanted to the Montane gardens for one or two years, has undergone alterations that cause it to resemble closely *caninum*. Under similar conditions, the inflorescence of *Luzula intermedia* has changed to be practically indistinguishable from that of *parviflora*, except as to the larger flowers. When the water of the habitat is increased to the point of providing for the mechanical stretching requisite for rapid modification, the habitual fixity disappears much more quickly, and several features may be changed during the first or second year after transplanting, especially in the shade.

This is especially true of the alpine species of *Senecio*. With *taraxacoides*, under watered conditions in the montane forest, the scape has become thrice elongated with 3-4 leaves and several heads, and the leaves 3-4 times normal length with marked changes in form and lobing. *Senecio croceus* has lengthened even more, with corresponding modifications of the inflorescence, head and leaves (Plates 80, 81).

Adaptations of similar intensity have occurred in other alpine species, such as *Veronica alpina*, *Erigeron uniflorus*, *Solidago virgaurea nana*, *Festuca brachyphylla*, *Trisetum spicatum*, *Luzula spicata*, *Thalictrum alpinum*, and *Campanula rotundifolia*. With the great elongation of the stem in *Sedum roseum*, go the extreme thinning of the fleshy leaves and the change of the flower-cluster from a cyme to an



open, panicle-like form, or in deep shade, to one or two flowers. When the alpine *Oxyria digyna* was grown in the full shade habitats of the montane spruce forest, the stems stretched to 3-4 times that of the dwarf at 12,000 feet. The petioles and blades were equally enlarged and the stamens suppressed (Plates 64-67).

Especially satisfactory have been such species as *Achillea millefolium* with an alpine segregate *alpina*, which has exhibited modifications of like intensity in favorable situations at lower altitudes but which has remained dwarfed in dry habitats, whether in the Plains Garden at 6,000 feet or in the Coastal Gardens at Santa Barbara (Plates 8, 68). Another example of the effect of low water-content at the same or different altitudes is that of *Carduus eriocephalus* which was found in moist spots of the alpine tundra as a thrifty plant although of low stature, and as a greatly reduced form in dry habitats at the same altitude. During an extremely dry summer at the Montane Station at 8,000 feet, this species appeared as a stemless rosette with a sessile cluster of flower heads. Nearby, under controlled factors of increased water and shade, the plants responded in the usual way to such influences (Plate 69).

**Clones.**—Unexpected results have been obtained with the clones of alpine species. It was assumed that these would grow slowly for a year or more, and that modification would be correspondingly retarded. On the contrary, they were fully established by the beginning of the second season and exhibited much change in a number of species, such as *Artemisia scopulorum* and *pattersoni*, *Erigeron uniflorus*, *Gentiana frigida*, *Trifolium dasyphyllum*, *Campanula rotundifolia* and others. More important than the actual changes, however, was the uniformity of behavior shown by clones of the same parent, from different parents of the same lots, and complete individuals transplanted in groups originally selected for their uniformity.

#### TRANSPLANTS FROM LOWER TO HIGHER ALTITUDES

While alpine species transferred to montane or plains climates, have changed but slowly or little unless placed in shade or extremes of water, montane species transplanted to 12,000 feet, have without exception undergone marked reduction. *Rudbeckia hirta* which grows normally to a height of 2-3 feet in the montane region, when transplanted to 12,000 feet, reached a height of only 2-3 inches with a few small hairy leaves and a single head with rays greatly reduced in size



Transplants from Higher to Lower Altitudes.

(Alpine dwarfs at right; adaptations to montane shade (8,000 feet) at left).

A. *Luzula spicata*

B. *Festuca brachyphylla*

C. *Trisetum spicatum*

D. *Thalictrum alpinum*



Transplants from Higher to Lower Altitudes.

(A, B, C, Native alpine dwarf at left; adaptation to montane shade at 8,000 feet, at right).

- A. *Sedum roseum*    B. *Erigeron uniflorus*    C. *Senecio taraxacoides*  
 D. *Veronica alpina*: 1. Montane shade; 2. Montane brook-bank; 3. Alpine dwarf.

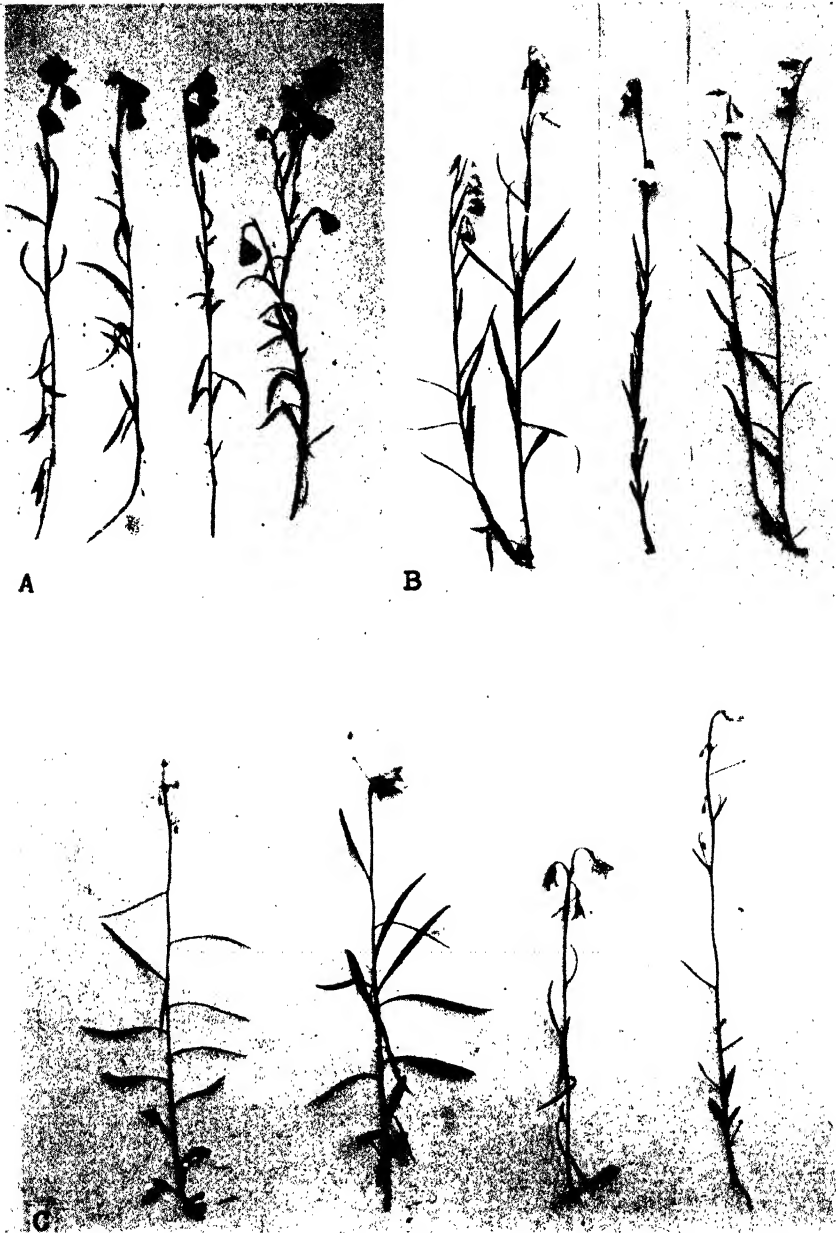


Transplants from Higher to Lower Altitudes.

*Campanula rotundifolia alpina.*

A. Native dwarfs at 12,000 feet: 4 inches tall.

B. Bed of transplants of alpine clones to Plains Garden at 6,000 feet;  
12-18 inches tall.



Adaptations of *Campanula rotundifolia alpina* Transplanted to Lower Altitudes

A. Single stems from clone transplant, Plains Garden (Cfr. Pl. 66).

B. Transplants to Montane Gardens: 1. Sun-moist; 2. Sun-wet; 3. Native *rotundifolia* control; dry shade.

C. Transplants to Montane Gardens: 1. Half-shade; 2. 20% shade in lath-house; 3. Sun-wet; 4. Native *rotundifolia*; sun-moist control.



Adaptations of *Achillea millefolium*.

- A. 1. Normal alpine dwarf; 2. Alpine dwarf after transplanting to Montane Garden; 3. Typical montane tall; 4. Montane form after transplanting to 12,000 feet; 5. Alpine dwarf in dry-sun at Santa Barbara (Cfr. Pl. 8B); 6. Drouth dwarf in montane dry-shade.
- B. 1. Alpine dwarf transplant in Plains Garden at 6,000 feet (18 inches tall); 2. Alpine dwarf grown from seedling in Plains Garden (18 inches tall); 3. Competition-form of normal plant in Plains Garden (19 inches tall).



Ecads of *Carduus eriophorus* at 8,000 feet.

A. 1. Alpine dwarf in dry soil; 2. Alpine dwarf in moist soil; 3. Sun-moist Garden; 4. Half-shade; 5. Full shade.

B. Plant dwarfed by dry season.

and number. At 8,000 feet during the same dry season which produced the drouth dwarfs of *Carduus*, two similarly stunted plants of *Rudbeckia*, appeared. These natural ecads, in addition to reduced stature, possessed characteristics that reflected the usual effects of light and shade, since one grew in open gravel and the other in the shade of the forest. The sun-form was stemless with a number of small rough hairy leaves and two small flowering heads, while the shade plant had a well developed rosette of large thinner leaves and a single sessile flower head (Plate 70).

In those species with natural alpine ecads, the transplants from lower to higher altitudes became practically indistinguishable from these in a single season. Such changes have occurred in a score or more of species such as *Achillea millefolium*, *Antennaria dioeca*, *Epilobium angustifolium*, *Dodecatheon meadia*, *Pedicularis canadensis*, *Pentstemon glaucus*, *Poa Pratensis*, *Smilacina stellata* and *Scutellaria resinosa*. These involve a four to tenfold reduction in the stem, a decrease of the leaves to a third or a fourth of the normal, a striking tendency toward a single flower or head, and a dwarfing of the flower. It is to be noted that these effects may be largely or wholly inhibited by shading, watering or fertilizing—factors which have already been demonstrated as effective in hastening the change of alpine dwarfs into typical montane species when transferred into such an environment (Plate 71).

From the foregoing, it is concluded that in the Pikes Peak region where the experiments in adaptation have been carried on, neither light nor decreased humidity explains alpine dwarfing, but that reduced water-content is the primary cause, although by no means confined to alpine regions. Where actual dwarfing occurs—that is the dwarfing of a plant which is found in the same water-content at two different altitudes, as for example, *Campanula*, *Achillea*, *Solidago*, etc., the efficient factors are low temperature, including shortness of season, and reduced pressure. The former seems to be somewhat more important but it is impossible to separate their effects in field experiments.

#### FIXATION

Strictly speaking, adaptation comprises only the change produced by ecial factors: fixation is its complement. The relation between the two is reciprocal, the degree of fixation setting wide or narrow limits for the operation of adaptation, and the latter in turn producing new





Dwarf Ecads of *Rudbeckia hirta*.

A. Dwarf form of normal species transplanted from 8,000 to 12,000 feet.

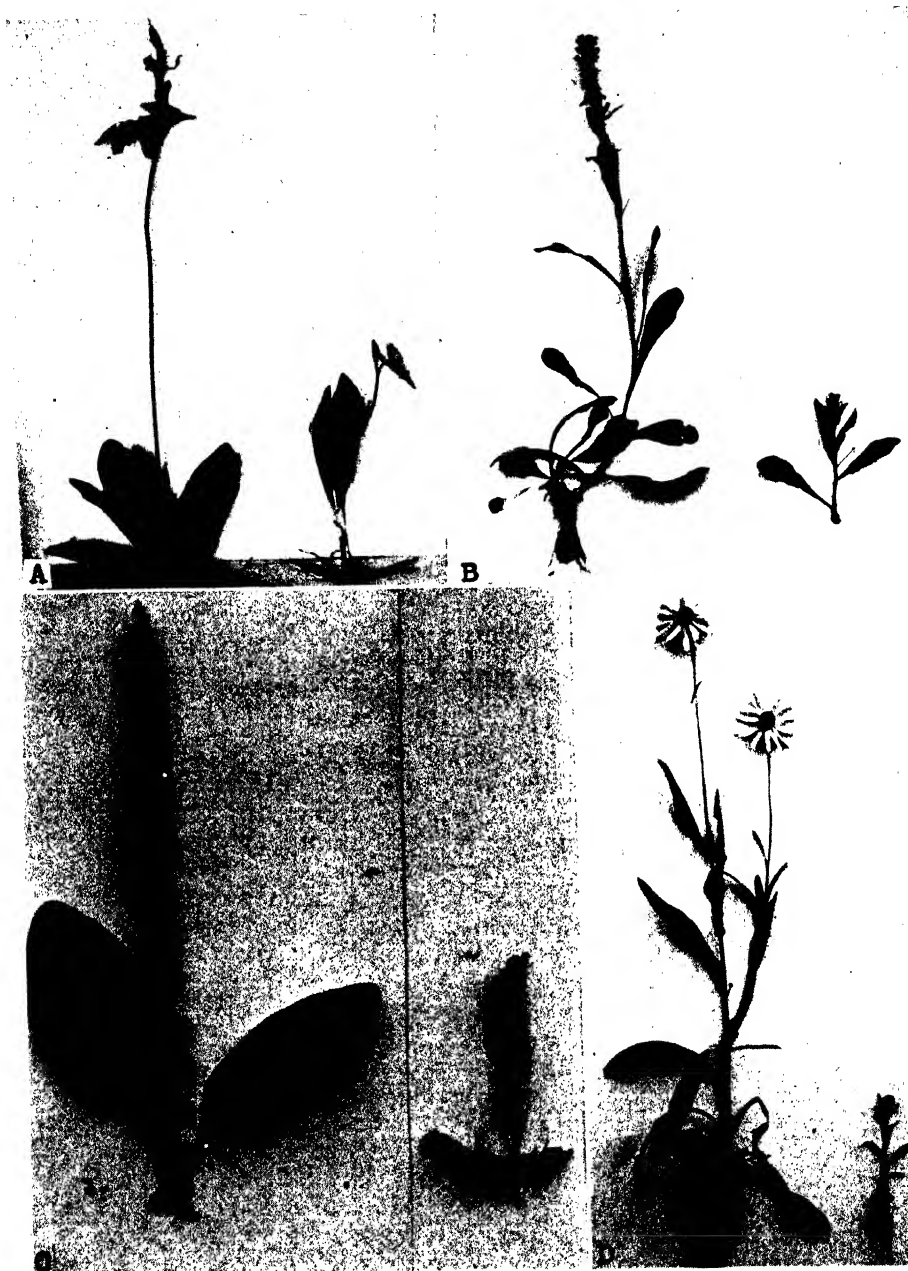
B. Dry season dwarf in montane dry gravel.

C. Dry season dwarf in montane forest.

features to be fixed. In consequence, it is helpful in experimentation to distinguish between fixity or stability and the active process of fixation. The former is readily investigated in the case of any species; the latter is the most difficult problem in ecogenesis and the technique for its study is being fashioned but slowly. The essentials of it are time and intensity, the one to be secured chiefly by increasing the number of generations in a year, the other by morphogenic manipulations that yield striking departures in a single season. In comparison, the inquiry into fixity is relatively simple, though this involves a critical analysis of the "expression" of characters.

Every experiment in adaptation affords a test of the fixity of the form concerned, but the evidence may be quite misleading. The fixity of many alpine dwarfs when moved from 12,000 to 8,000 or 6,000 feet has appeared complete, owing to the substitution of one efficient reducing factor, drouth for another, cold. The two habitats, though widely separated in altitude, are essentially identical in effect. Somewhat similar behavior has been exhibited by reciprocal transplants between sun and shade or wet and dry areas. Many of these transfers are ineffective, because the degree of change in factor lies within the growth response, and actual modification of form is secured only by greater differences, as the successful transplants demonstrate. The effect of time is also evident in most of these, the adaptation accumulating with each season, exhibited especially in *Erigeron glabellus* moved to the dry sun habitats of *macranthus*. Even more striking is the case of *Artemisia vulgaris gnaphalodes* transferred from dry sun to deep moist shade; the early leaves and young shoots bear the characteristic white tomentum but this is greatly reduced in the later leaves, almost to the point of disappearance.

Gardens of the usual mesophytic type have proved likewise more or less neutral in effect with respect to changes of form, and consequently afford slight or misleading evidence as to fixity. This holds for the mesophytic species, but not for the xerophytic or hydrophytic ones, for which such gardens furnish fairly extreme conditions. The assumption that growth is directed by mean conditions and modification by extremes has been verified so regularly as to constitute a helpful working basis. All the results so far obtained in this connection indicate a certain degree of inertia in each species, corresponding apparently to its habitat and experience. Holarctic species of great age, such as *Silene acaulis* and *Androsace chamaejasme*, remain practically



Transplants from Lower to Higher Altitudes.  
 (Normal montane species (left) ; alpine ecads (right)).  
 A. *Dodecatheon meadia*  
 B. *Solidago humilus*  
 C. *Besseyia plantaginea*  
 D. *Rudbeckia hirta*

unchanged at all altitudes employed, but they are easily modified by deep shade. *Paronychia pulvinata*, an alpine cushion-plant with flowers and leaves at the surface of the soil, develops under shade into a form with slender leafy stems, closely resembling *jamesi* of much lower altitudes, while *Silene acaulis* underwent a like metamorphosis, to suggest one of the stemmed European species of the genus (Plate 63B). Alpines of more recent origin respond much more readily and undergo considerable change in the altitude gardens, while the alpine varieties of montane and subalpine species often resume the form of the parent in a single season. It has already been said that fixity is less in evidence in transfers to the alpine zone, a fact apparently related to extremes of more than one factor. It is also hoped that this complex of extremes will furnish a promising approach to the problem of the actual fixation of new characters. Finally, it appears that alpine dwarfs, like other ecad groups may lose their fixity gradually through several years, partly through the duration of the stimulus and partly in consequence of the seasonal swing involved in annuation.

#### HYBRIDIZATION

**In Nature.**—In the endeavor to throw light upon the role of hybridization in the origin of new forms in nature, a comprehensive investigation was initiated in two different floras. The flora of the Pikes Peak region is generally boreal in nature and hence representative of circumpolar lands, while that of southern California is largely austral and peculiar to the Southwest. The major objectives have been the systematic examination of each flora for hybrids, the genetic analysis of genera long supposed to produce hybrids in nature, such as *Verbena* and *Aquilegia*, the production of hybrids between native species, and the behavior of the meiotic mechanism in representative cases.

The scrutiny of the native flora is based upon the criteria established by Rosenberg and extensively employed in America by Jeffrey and his students. These consist chiefly of the imperfection of the meiotic apparatus and a high percentage of sterility in the pollen, often accompanied by striking variability and exceptional vigor. All the species of families known or suspected of hybridizing readily have been examined for imperfect pollen, and material taken for the study of meiosis, such as *Oenotheraceae*, *Verbenaceae*, and *Ranunculaceae*, etc. In connection with this, an attempt has been made to produce sterile pollen experimentally, to serve as a check upon its occurrence in nature.

It has been found that morphogenic manipulation sometimes results in poor pollen, even when the stamens are otherwise normal.

In the direct examination of the native communities for possible hybrids, the most striking instance has been that of *Mentzelia*. A large number of intermediates between *multiflora* and *nuda* were found mixed with the latter parent and with forms distinguishable from *multiflora* only in stem color. The color of the flower ranges from the white of *nuda* through various shades of yellow, only rarely reaching the orange-yellow of *multiflora*. Stem color and pubescence are usually that of *nuda*, while the leaves run the entire gamut between the two. The pollen of this supposed hybrid shows the widest range, from 95% sterile to 95% perfect, without exhibiting any correlation with resemblance to either parent, both of which have perfect pollen. Reciprocal crosses of the parent and back-crosses with the hybrid have been made in the community itself and also in the Plains Garden.

No natural hybrids of *Pentstemon* have been found, with the probable exception of *parishi* in California and a form of *unilateralis* in Colorado, in addition to *spectabilis* X *centranthifolius*, where the field evidence alone appears nearly conclusive. More than 50 species of *Pentstemon* have been grown in both the California and Colorado experimental gardens, and several hundred selfs and crosses have been made. While it is evident that many of the species can be crossed by hand, there has been no proof that any of the native species, with the exceptions noted above, are the result of hybridization.

**Under Control.**—An endeavor has been made to develop a complete system of experiment in connection with the pollination and fertilization behavior of selected species, based upon the previous researches in experimental pollination (1923). This involves allogamy and autogamy under both natural and artificial conditions, as well as crossing under control and under methods of contiguous and mixed planting that stimulate the opportunity in nature. The development of a technique suited to nature and to semi-natural gardens has presented peculiar difficulties such as the danger of a large rodent population, etc. The studies of autogamy have afforded some important by-products, first in providing more uniform material for studies in ecogenesis, and second in furnishing evidence that self-pollination in nature is much less effective than has been supposed.

The initial studies dealt chiefly with *Pentstemon*, *Aquilegia*, *Oeno-*

*thera* and *Geranium*. *Pentstemon* offers especially favorable material from the standpoint of the large number of species available and the success with which they can be handled in semi-natural and control gardens. Moreover, none of the local species have been found to produce imperfect microspores, and it seems probable that the cytological study will show that these are not hybrids. On the other hand, numerous garden hybrids already exist between several of the native species of *Aquilegia*, thus permitting the desired twofold attack upon the genetic constitution of these as well as upon the production of hybrids under known conditions. Apart from its well-known behavior in the section *Onagra* and the interest attaching to the relation between mutants and hybrids, *Oenothera* affords an attractive focus for experiment because of the unusually large number of well-marked sections and the fact that these have often been regarded as distinct genera. Studies have also been made of certain reciprocal species transplanted for adaptation and fixation, such as *Geranium caespitosum* and *richardsoni*, from which selfed seed and reciprocal crosses have been obtained.

**Methods and Results.**—The pollens examined have been stained by the method employed by Belling, which insures an accurate determination of sterile grains. The species have been divided into three classes: (1) with 50% or more of the pollen-grains imperfect; (2) with 20% to 50% imperfect; (3) with less than 20% imperfect, few species producing more than 95% of good grains. Of the 6 species in the first class, 3 belong to *Potentilla*, 2 are alpine, and one *Oenothera speciosa* grown in gardens. Five of the 18 species in class two belong to *Oenothera*, 3 to *Gentiana* and 2 to *Rosa*. Eight of 10 species of *Pentstemon* gave percentages of 90-95, the other 2 dropping to 65%.

Further evidence of hybridity has been sought in selfing approximately 200 species, many of them for 3-5 generations, and attempts at crossing have been made in not a few. Between linneons, crossing has yielded negative results in all but a single case, namely, *Godetia amoena* x *grandiflora*, and selfing has furnished no evidence of hybridization in the species used. Some work has been done in the way of genetic analysis of ecads as well as hybrids, but time and facilities were lacking to pursue it to a satisfactory conclusion.

The work of Rosenberg, Tackholm, Longley and Jeffery in particular, seems to indicate that mutants in the DeVriesian sense, are all hybrids or "hybrid-mutants." Since characters must originate be-

fore they can be combined in hybridization, or species actually hybridize themselves, this is further evidence that adaptation or ecogenesis is the universal process of primary origin, and hybridization of secondary origin from the primary. Hence the first task in analyzing a natural flora is to distinguish between the ecogenic or primary species in this sense and the hybrid or secondary. Pollen character should permit this without complete genetic analysis, although this should follow sooner or later in all cases.

The criteria noted by Jeffery for hybrids, namely vegetative vigor, variability, reproductive loss or sterility, imperfect pollen, and faulty mitosis, are those already suggested on ecological grounds for regarding *Oenothera*, *Datura*, *Bursa*, *Crepis*, and *Drosophila* as overnourished ruderals with a terad constitution in all probability. Perhaps hybridization is to be regarded primarily as a nutritional (chemical) rather than a genetic disturbance directly.

On this basis, variation and mutation are all the more extremes of the same process, but there are quantity differences in hybridization as well as in adaptation, and probably also in teratogeny. In short, ecads, terads, and hybrids all may exhibit small differences or sudden large ones, such as may well be called "hybrid-mutants." Thus variants and mutants become mere quantitative terms for use in connection with ecogenesis and hybridization and probably also teratogenesis as a third method of origin distinct at least from adaptation to physical factors.

#### STOMATA AS INDEXES OF ADAPTATION

**Methods.**—While instruments serve as an indispensable background against which to project responses to the direct factors as well as the factor complexes, phytometers give a much more significant expression to that of specient and community. In addition to the correlations already noted in the way of growth, function and form, the number and behavior of the stomata have proved to be one of the most sensitive indexes of adaptation when applied to the garden experiments. The daily cycle of opening and closing is an especially delicate measure of conditions, to the final extreme in those hydrophytes in which the stoma is more or less permanently open.

The methods employed to secure the data indicated, are direct vision with laboratory microscope in plant-house or garden and hand microscope in the field, stripping the epiderm and plunging it in absolute alcohol, and coating the leaf surface with collodion or some

similar form of nitro-cellulose. The films are easily preserved and transported as dry mounts, and are available for study at a moment's notice. In species with a fair range of stomatal opening, they give promise of replacing epidermal strips to a large degree.

**Applications and Results.**—The method has been extensively applied, not only to the adaptation results in the control and field gardens at Santa Barbara and Pikes Peak, but it has been widely utilized in the endeavor to obtain norms of stomatal behavior in a number of different climaxes and seres in the course of the ecological reconnaissance of desert, grassland and forest associations. During a field trip from the Pacific to the Atlantic by a northern route, and the return by a southern one, many hundred paired-films of climax and seral dominants and subdominants were secured with the twofold objective of determining the stomatal relations for life-forms and communities, as well as for genera. This large series of films and the range of communities has given a quasi-experimental value to the field studies and brought to light a number of novel correlations.

The use of such collodion films for obtaining a quick and permanent record of the number and distribution of stomata promises to supplant entirely the method of epidermal strips, though this and direct vision will probably always remain indispensable for aperture studies. The collodion film, moreover, is applicable to leaves and upper surfaces not capable of being stripped, and it avoids the obscuring effect of a torn mesophyll. Not the least of its virtues is the fact that an initial film can be employed to remove a coating of hairs and a new one then applied to secure the stomatal impression. Its rapidity and certainty of operation render stomatal transects, crosswise or lengthwise of the leaf a simple matter, and thus permits much more comprehensive and accurate counts (Clements and Long 1924).

In the adaptation and transplant gardens, especial attention has been paid to the number and distribution of the stomata, and in the 24-hour cycle of stomatal behavior. As a general rule, the number was closely related to the conditions for growth, decreasing per unit area as growth and expansion increased. In the case of light, however, and with certain species in the water and nutrient series, leaf expansion was greatest in median conditions, and the number of stomata greater at the two extremes. In some cases, the inverse relation did not hold between growth and number, indicating a more deep-seated modification of the meristem (Table 47).



## CHAPTER IX

### EXPERIMENTAL MORPHOGENY

**Definition.**—This term is intended to include not only experimental morphology, which owes its organization chiefly to Goebel (1900, 1908), but especially also the fields of correlation and teratogeny which have received much less experimental attention. Under the name of teratology, ("terad" from *teras*, monster), a vast number of pelories and other monstrosities have been described and classified, but no thought has been given to the ecological study of these. The analysis of the causal relations, the measurement of factor and function, the intimate physiology of cell and tissue, the artificial duplication of natural monstrosities as well as the induction of new ones, and the evolutionary and phylogenetic significance of all this have been too largely ignored. In the present investigation an attempt has been made to coordinate the several objectives, refine and extend the various methods, and to utilize experiment and measurement as the two fundamental principles. Natural experiments take an essential role in this along with control and induced ones, while an adequate background demands the study of the normal morphology of a large number of species and genera peculiar to the New World. For a number of reasons, the experimental attack has been focussed chiefly on the flower and fruit. This not only yields results of permanent significance for evolution and phylogeny, but it likewise opens up the whole field of somatic and genetic correlations and thus permits the causal comparison of the two great sets of factors, eci al and physiological.

While Goebel is correct in stating "that it is impossible to frame a generally applicable definition to the notion of malformation," a good working basis is afforded by the view of Darwin that a monstrosity is marked by some considerable deviation of structure, and of Moquin-Tandon that it consists of any extraordinary deviation in the formation or development of organs, irrespective of any influence upon health. Goebel considered that malformations are necessarily connected with disease, and Darwin regarded them as generally injurious or at least not useful. This is obviously a matter to be determined in each instance, and it already appears certain that many malformations are neither harmful nor useless.

Experimental morphogeny has much in common with adaptation and fixation, but at the same time supplements these in a most effective manner. The stimuli employed are under much more definite control and the course of response can be traced with greater exactness. The focus of attack is nutrition in the wide sense and this promises to afford a direct approach to the correlations between soma and germ and the biochemic processes involved. Some natural malformations or terads are fixed and others are not, a fact that seems to be equally true for the much smaller number of induced ones. The increasing ease and rapidity with which terads may be induced indicate the early accumulation of a large mass of material, not greatly inferior in amount to that produced by adaptation, and much superior in its immediate value for studies of fixation.

**Methods and Materials.**—The materials selected for the present series of investigations have been chiefly native annual and perennial herbs of considerable vigor and growth. These have been chosen in such a way as to represent the great ecological groups of choripetalous, and of insect and wind-pollinated flowers, with a special predilection for those in which parts have been greatly transformed or lost. Every conceivable factor has been employed to produce abrupt and striking modifications, from overdoses of habitat factors on the one hand, to the injection of various solutions on the other—foods, enzymes and hormones being most favored because of their direct relation to metabolism.

Excision has been one of the most effective methods, though results have been secured from all those that produce hypertrophy or hypotrophy. Vigorous growth has usually proved to be an essential, and for this reason, plants just budding have yielded better results than those in full flower. This probably also explains the greater success with cultivated species and with free individuals rather than those in competition groups. The basic significance of nutrition in practically all cases is shown by the fact that drouth, competition, rust, aphids, or constrictions of the stem may be used to produce essentially the same effect (Plates 72, 73).

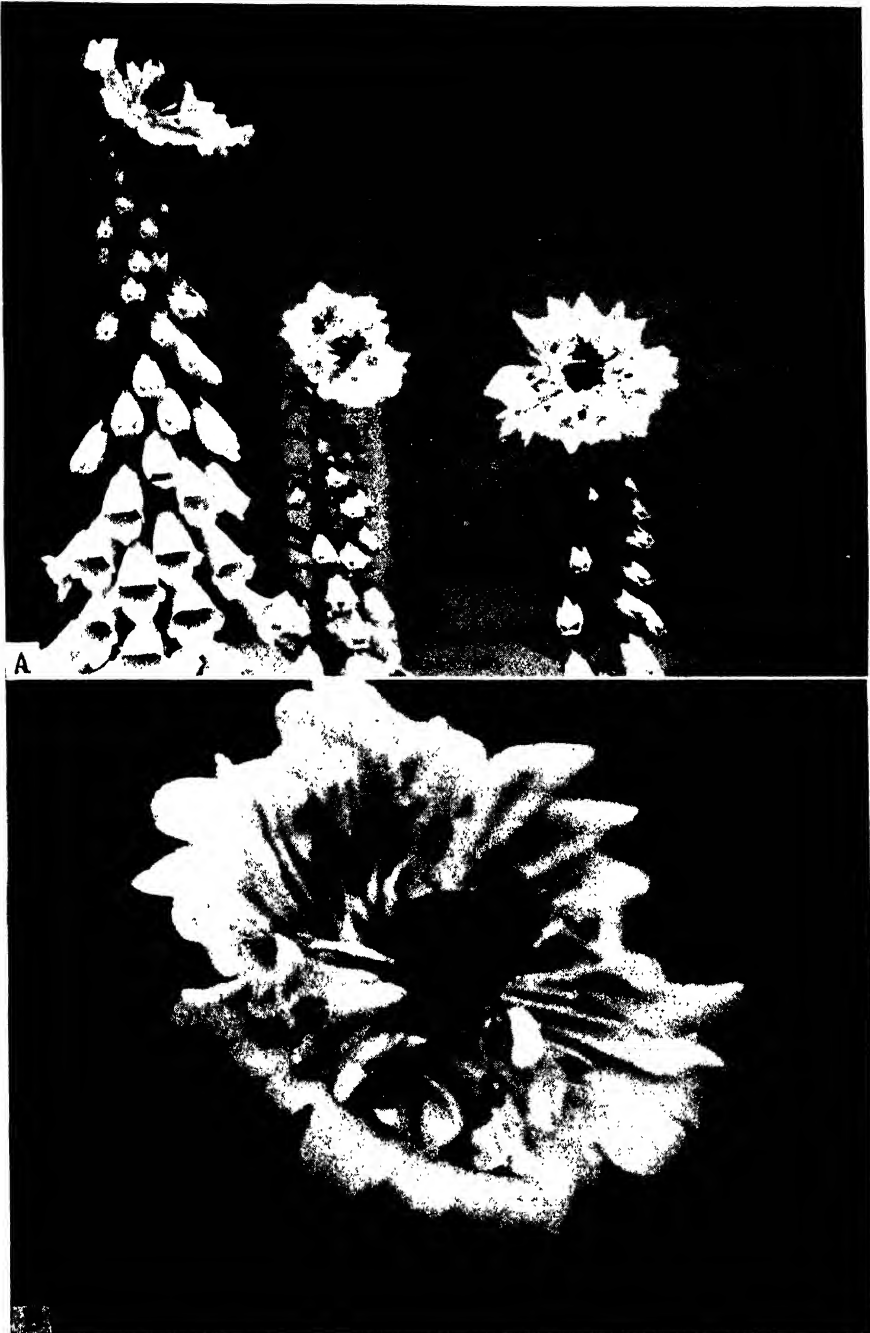
**Competition and Correlation in the Plant Body.**—The background for the experiments in competition between the different organs and parts of the plant body and their correlated development, has been furnished by extensive observation of buds and flowers under normal

and abnormal conditions. The experimental methods have been concerned chiefly with changes in position of all sorts, removal of one or more parts in varying number and under various conditions, girdling, wounding and compression, the insertion of buds or other parts, and the addition of physiologically active substances such as water, sugars, nutrients, salts, acids, etc. The experiments have also been combined in diverse fashion in order to furnish checks upon each other and have been repeated in different seasons and years for the same purpose, as well as to exhibit the range of behavior. An endeavor has likewise been made to follow the storage cycle in close detail, to discover its precise relation to growth, and to determine the variations in it from season to season.

Four years of observations on erect, horizontal and hanging twigs of *Populus* and *Prunus* indicated that tip buds developed first regardless of position, and this was confirmed by the behavior of shoots purposely inverted. In the cottonwood, leaf and flower buds, both staminate and pistillate, behaved alike, the tip buds of hanging shoots starting first in 99% of all cases. Removing buds from the tip downward regularly forced the next buds into growth, as did the removal of part or all of the last three seasons' growth in *Melia*, but the excision of intermediate buds was without apparent effect. Notching twigs on both sides above or below buds was ineffective, but constriction by means of wire bands, led to development in 2 to 4 buds immediately below, while the same buds on check shoots remained suppressed. Stripping portions of the bark and wounding in other ways also produced growth, usually below and more rarely above the injury.

In feeding glucose to suppressed buds, series of four adjacent ones were employed: a tube of 1% glucose was inserted above one bud and below a second, a tube with water above or below the third bud, and a gimlet wound made in the vicinity of the fourth, the wound being filled with moist cotton and wrapped with tape to prevent drying. The buds responded to glucose in every case, whether inserted above or below, and in most cases to water alone, but not to wounding. Water had failed to produce a response the preceding year, and the positive result was probably due to the much more advanced condition of the twigs. In similar groups of four, glucose and sucrose yielded almost identical results, the growth varying somewhat with insertion above or below the bud.

In the experiments with flowers, the hoard or light intensity was



Terads of *Digitalis gloxinoides*.



Terads

- A. *Baptisia leucophaea*: 1. Normal raceme; 2. Terad.  
 B. *Psoralea tenuiflora*: 1. Normal plant with 3 leaflets; 2. Aecidium terad with 5 leaflets.

modified within wide extremes, producing a direct effect in the shoot and a correlated one in the inflorescence; flowers and heads were modified by the excision of various parts, and the different organs and parts were subjected to the action of various solutions injected by means of a Luer tuberculin syringe. In many cases, these produced striking effects. With *Campanula medium*, allowing the plants to wilt and dry for 3 weeks after blooming and then watering abundantly threw suppressed flower buds into vigorous growth and resulted in doubling the corolla, 4 to 5 additional tubes developing outside the usual one.

**Natural Mutants.**—Variations in the number-plan of *Verbascum blattaria* have been followed in great detail for two years, and one generation has been obtained from terad parents. In 1926, flowers with 6-parted corollas were borne on the main axis and they were produced more abundantly during foggy periods. Plants sown in the spring of 1926 that did not bloom until 1927, became unusually large and vigorous, and produced more 6-parted flowers than any others, the majority appearing in the lower third of the spikes, on both the main axis and the laterals. Removing the upper two-thirds of the main spike increased the number of sixes, as did also removing the two lateral buds of each cluster of three. The first five days of blooming yielded 8 times as many terads as normal flowers. By June 14th, a month later, the main axis had practically ceased producing terads, but half of the 50 or more flowers opening each day on the laterals were 6-parted. After this time, the number and percentage of the "sixes" fell rapidly, flowering ceasing by the middle of July. Throughout both seasons, the production of such flowers was increased by factors of light and water that promoted growth, and it was significant of the times and of the portions of the plant in which nutrition was greatest.

Climate and season seem to have an evident effect upon terad production in a number of other cases. *Sisyrinchium bermudianum* developed number-terads to the extent of 50 percent of the total, while other species native to the region gave none. Both *Datura tatula* and *stramonium* exhibited profound changes in the fruit on nearly all plants from early summer to autumn. This consisted in a progressive reduction in the size in late summer, and in the number and length of the spines, until the last fruits were reduced to a fifth of the normal and were nearly or quite smooth. After flowering normally and the

fruits had dehisced, large plants of *Oenothera biennis* were heavily watered. They put forth numerous short flowering branches in the midst of or at the base of the dry inflorescences, or more rarely produced corymbs of flowers at the tips. The flowers were a third or a fourth of normal, the tube very long and slender, the stigmas closed and included in the throat.

### MANIPULATION OF THE PLANT

**Mutilation.**—The successful production of terads or anomalies has been found to rest in the first place upon the vigour of species and plant, and in the second upon the timing of the mutilation. Vigour is obviously directly related to nutrition and to regeneration, while the rhythm of growth seems to be such that treatments successful at one time are without effect at another. Most manipulations can be classed as traumatic, though some are only incidentally so. They may operate directly upon the plant body or upon the flower and fruit, though usually the most interesting cases are those in which the manipulation of the shoot finds its chief expression in the flower. They may also be grouped with respect to the effect upon nutrition, in accordance as the food-supply to a part is increased or decreased. Manipulations are further distinguished on the basis of the method used or the part affected.

The most successful method has been the removal or cutting back of shoots, especially the shortening of the main axis, and the excision of buds or flower-parts. All these involve an increased supply of food to the parts that remain, with the resulting tendency to disturb the normal development. Such manipulations may be regarded as traumatic, but merely wounding without a marked deflection of the food-current has never been found to produce considerable effects in the species tested. The relative length, amount or number of the part or parts removed is decisive, severe pruning being much the most effective as a rule. When severe mutilation is undesirable at the outset, good effects have sometimes been secured by progressive pruning.

Many devices have been used for reducing the food-supply to an organ or part, but they all fall into a few categories. These are defoliating, bending or breaking over the axis, and constricting or girdling the stem. In general, these are much less successful than the methods that increase the nourishment, but they deserve a place in the complete system. However, this does not apply to the coactions

of insects or fungi, many of which produce the most striking malformations and are susceptible to experimental control (Plate 73B).

The striking changes produced by mutilation are well illustrated by *Frasera speciosa* growing in the open forests of the Montane Station in Colorado. Cutting the stem back to the two lower nodes led to the development of flowers in these, most of which were abnormal. In one case, the flowers were merely enlarged to about twice the normal size; in another, the number-plan was affected, and in the third, one or more of the stamens bore one or sometimes two petaloid outgrowths, usually without affecting the pollen. In a few flowers, the stems were reduced to vestiges. These plants were in the same stage, grew near each other in the same habitat and were treated alike at the same time, but in spite of this yielded very different results. When all the buds of the primary clusters but the two youngest were removed, the flowers were often formed on the plan or 2 or 3, though none of these developed in the untreated clusters. Reduction of the flower to a third or fourth of the normal was not infrequent, and in these, the nectaries and covering scales were sometimes greatly changed (Plate 74A).

Similar changes in size and form were especially common in *Castilleja miniata* as a result of pruning, bending the stem sharply or removing all the leaves. The reduced flowers were replicas of those of the variety *parviflora*, often regarded as a species, though in extreme cases they became much shorter and to a large degree cleistogamous. In the case of *Thalictrum sparsiflorum*, compression of the stem reduced access of food to the flowers and in consequence the pistils failed to develop. This strongly suggests the manner in which the dioecious *fendleri* of the Rocky Mountains was evolved from the circumpolar *sparsiflorum* with bisexual flowers. Bending the stem of *Epilobium angustifolium* in such a way as to reduce the food-supply towards the upper part of the inflorescence, resulted in the production of small albino blossoms beyond the bend.

**Injection.**—Injections of glucose into tissues, increases the food-supply to some degree, but the resulting changes seem to be due rather more to the osmotic effect. Solutions of various kinds, namely, acids, alkalis, salts, enzymes and hormones have been injected to yield terads of varying form and degree. Injections have rarely been successful except when applied to young flower-buds or made in peduncles,



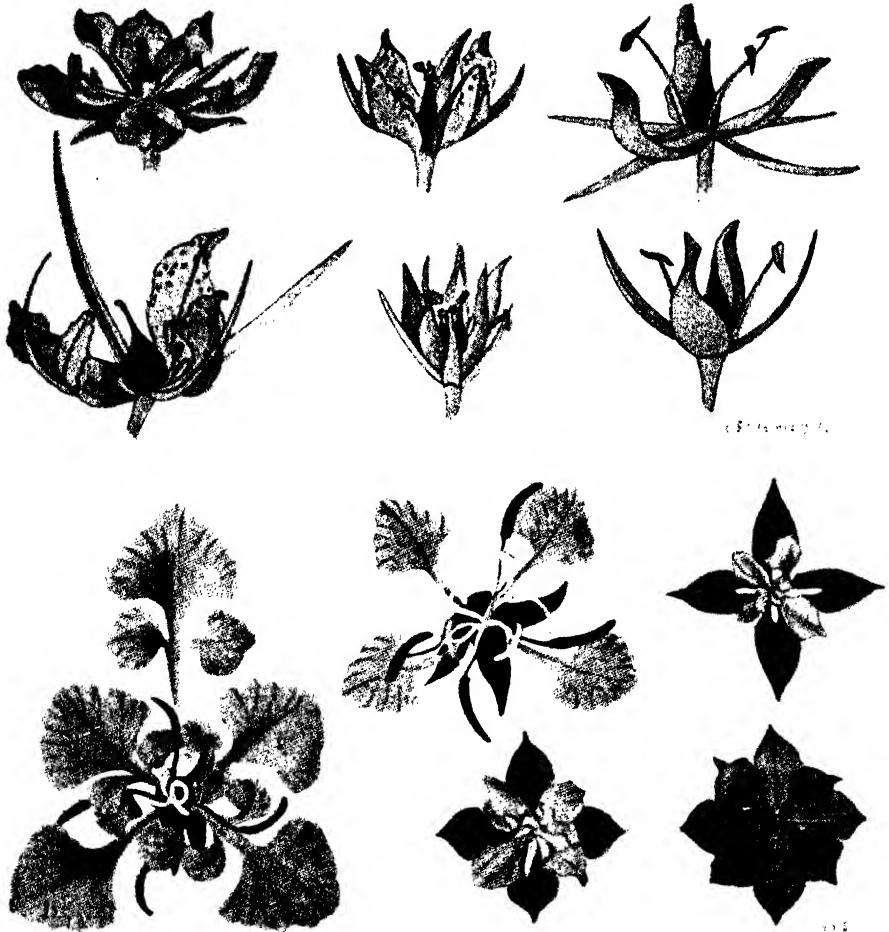
probably owing to the small amount of solution that can be taken up by the inelastic tissue. In the case of glucose, the regular method is to use tubes drawn out to a fine point, which can be attached to the shoot and kept filled with the solution.

As a rule, injection when effective, is expressed in changes of size and color, but in a few species it has had a much more pronounced result. The use of dilute solutions of honey or dextrose led to reduction of the corolla in *Salvia grandiflora*, often with much suppression of the lips and to sterility and abortion of the anthers. In *Clarkia elegans* (Plate 74B), it produced the splitting of one or more petals, giving a doubling effect, a process also brought about by the use of inorganic solutions, such as 1 percent of acetic acid, potassium permanganate, etc. The injection of honey into the buds of *Oenothera biennis* resulted in cleistogamy in every case, but was without effect in the larger buds of *O. lamarckiana*.

#### MANIPULATION OF THE HABITAT

**Hypertrophy.**—It is evident that hypertrophy is much like the change or inversion of habitats for calling forth adaptation, but it is designed to affect nutrition as directly as possible, usually in terms of over-growth. In the case of most natives and many ruderals, tillage alone may be counted upon to produce some anomalies, but even these, and particularly with cultivated species, the skilful use of water or fertilizers is much more productive of change. The direct application of glucose to the soil in a way to insure its reaching the absorbing roots has also been tried, but its success is still doubtful. Hypertrophy artificially produced in *Helianthus annuus* caused the appearance of a raceme of small heads in place of a single large one, the reduction of the imbricated involucre to a single row of bracts, and the complete loss of the rays (Plate 75).

Probably the most illuminating results have been obtained with *Plantago lanceolata*, two similar and typical plants of which were transplanted from a roadside to the Santa Barbara garden in 1925. They were left without cultivation, but the seedlings grown from them in 1926 were tilled and watered, and subjected to considerable competition. The adults became greatly overgrown, reaching a height of nearly three times that of the field-plants and bearing dense rosettes of very large leaves. Some of the plants bore a central spike with a cluster of small ones at the base, others produced a cluster of leaves



Terads Induced by Manipulation.

A. *Fraxera speciosa*

B. *Clarkia elegans*



A



B

Terads of *Helianthus annuus*.  
A. 1. Normal head; 2 Terad induced by hypertrophy.  
B. 2. Detail of induced terad.

resembling an involucre, and still others showed a marked tendency to become unisexual. Open seed was collected from the various terads, and adult plants of each were transferred to a new bed to reduce competition. In 1927, no involucrate heads were borne by these transplants, but one or two plants yielded only large, greatly compounded spikes, while another produced only spikes with pistillate flowers for a time, and then an occasional spike with staminodes also. Seed from plants of 1926 with much elongated spikes or those leafy at the tip, gave only normal individuals, except for a few doubled spikes, while those with involucrate spikes exhibited but 2 such in 1200. However, a new terad, an umbel of 5 separate spikes, appeared in this progeny, and there was a tendency for all beds to produce a form with small yellow stamens containing but a small amount of pollen. Seed from extremely compound spikes yielded 129 such spikes out of 1200, practically all of these on 7 plants out of 100. When spikes were extremely compounded, all the spikes of a plant were of this sort, but mere double or slightly compound clusters were restricted to 1 or 2 on normal plants.

Other mutations comprised the appearance of a number of bracted and of multiple spikes, developed chiefly as a result of hypertrophy brought about by optimum conditions. The following year the stamens became abortive in 2 plants, producing a pistillate form with included staminodes. In the next 2 years the same form has developed in half a dozen other cultures, usually with an exact intermediate between it and the normal plant with perfect flowers. A noteworthy terad is composite in type, each flower being represented by a tiny spike of buds, remaining closed except for an occasional normal flower. In another, the flowers are few and each is borne on a long delicate pedicel resembling a filament. In the case of clones of a pistillate terad, about half the spikes on each plant became bifurcate or more rarely trifurcate about the middle (Plates 76, 77B).

A striking instance of animal causation has been exemplified by a plant badly infested with slugs, in which the stature is that of a dwarf, the leaves filamentous and chlorotic, and the spikes globose, but with 1 or 2 normal flowers. The marked plasticity of the species is perhaps best illustrated in the competition cultures in which the suppressed individuals are a few inches tall with small leaves and spikes, and the dominant ones 4 to 5 feet high, with leaves 1 to 2 feet long and spikes 4 to 5 inches in length (Plate 77A). In spite of the

difficulty of securing selfed seed from terads, and especially pistillate ones, the progeny of several have been grown to determine the fixity of each form, and in a number of cases this has proved unexpectedly high. For the production of a particular terad, it rose as high as 50 percent and for the process itself, involving 2 forms, it was as high as 85 to 100 percent in the water series. There is further some preliminary evidence to indicate that the degree of fixation increases from year to year.

**Hypotrophy.**—As an outcome of decreased nutrition, deep shade now and then produces terads, and these are more frequent consequences of the reaction upon water, light and nutrients arising from competition. Similar but less definite relations are concerned in out-of-season blooming, either early or late, and in photoperiodism, both of which are concerned with the light-heat supply in photosynthesis. In *Gaillardia*, hypotrophy resulted in the elongation of the receptacle, the loss of ray-florets, the separation of the bracts and the development of a disk-floret in the axil of each, as well as the change of the fringed chaff into herbaceous bracts. The most thorough-going transformation among composites, however, was obtained in a native species of California, *Agoseris aurantiaca*, which yielded a complete series from plants with normal heads to those in which the florets exhibited a greenish paleaceous calyx, a setose corolla, and abortive stamen-ring and an enormously elongated style and achene. In such plants the latex was totally absent, a significant departure from the universal rule in *Cichoriae*.

In the conical heads of *Lepachys columnaris*, there was a shortening of the axis, though the causal relations were complicated by the presence of aphids. In addition, the ray-florets exhibited various gradations to green leaves, the disk-florets were borne on long stalks, the stamens were abortive, and the style-branches long exserted and green like the corolla.

Finally the habitat may be manipulated by using water as a medium for the production of cleistogamy or related changes, or by employing light, gravity, or both, in connection with induced zygomorphy or actinomorphy in the flower.



Terads of *Plantago lanceolata*.



*Plantago lanceolata.*

A. 1. Normal plant; 2. Competition dwarf.

B. "U-terads" produced by hyertrophy in the Shelter Garden.

## CHAPTER X

### PHYLOGENY

#### PHYLADS

The value of adaptation cultures in producing objective results has become increasingly evident and is best exemplified by the phylad. This term denotes a continuous *phylum* of species, suggested by variads and ecads in nature and confirmed by manipulation in the gardens—an evolutionary *continuum* in short. It consists of two or more species, one of which is ancestral or basic and the others derived. As a rule, phylads are suggested by close morphological resemblance, but they are also revealed in increasing number by experiments in ecogenesis. Each phylad permits experimental study from either direction in the major task of determining the ancestral species and the course of evolution, but the derived species has usually appeared more susceptible of modification. Quite apart from the objective nature of the evidence, a signal advantage of the phylad method lies in the opportunity to analyze the phyletic lines of larger groups, such as genera and families, especially where the continuity is good. As a result of careful morphological study, such a line may be divided into its probable phylads, all of which may be tested simultaneously by means of experiment. When the even more effective methods of experimental morphogeny are added to those of ecogenesis, it becomes possible to bridge the gaps between some orders at least and to place their sequence upon a more and more objective basis. The phylad thus constitutes the open sesame to the understanding of the interwoven problems of migration, evolution and phylogeny as determined by great climatic changes.

**Lupinus Phylad.**—Among the genera of forbs employed in experimental adaptation (ecogenesis), *Lupinus* is representative of those of wide extent, great abundance and marked powers of survival and adaptation. Perhaps no other genus of forbs in Western North America equals it in the great number of intimately related ecads. On both the Great Plains and the Pacific Coast, occur an annual and a perennial phylad, those of each life-form doubtless stemming originally from a single species covering the entire area. In California, the perennial stock has become differentiated into a coastal—usually a dune—series,



and a montane one with a corresponding tendency to woodiness. The annual phylad is logically a denizen of warm valleys and desert plains, and in consequence has undergone even greater differentiation because of its greater adaptability. Both of these agree in the fact that the taxonomic division into species is largely based upon the technical character of the distribution of hairs or cilia on the keel of the flowers. This proves to be a reversible character, almost as easily gained as lost, and hence one that contributes readily to the conversion of species. As a consequence, it has been possible to trace a continuous phylad in both the annual and the perennial groups by combining garden and field results, and the immediate task is the usual one of discovering the complete phylad in nature, as well as by reconstituting it by experiment.

**Mertensia Phylad** (Frontispiece).—*Mertensia* is also one of the most plastic genera and in the experimental gardens on Pikes Peak has yielded a large number of conversions, in addition to many cases of convergence within the phylad. The four major species, or *linneons* of Lotsy, bear the clear impress of their respective habitats and hence are sharply contrasted with each other. The circumpolar *Mertensia sibirica* is evidently the ancestral form, growing by preference along brooks in the forest edge. From this have apparently sprung the paired species, *pratensis* and *lanceolata*, the one adapted to the shade of spruce forests, the other to full sunshine in meadows at the same altitudes. The origin of *alpina*, a typical dominant of the alpine tundra is less manifest, though the mutual convergence between it and *lanceolata* under experimentation suggests a direct evolutionary connection with the latter rather than with *sibirica*.

#### CONVERGENCE AND CONVERSION.

**Significance.**—Direct adaptation produces new forms, usually within the variation of the species; conversion deals with the transformation of a species into a closely related one, at least as far as morphological and functional criteria are concerned. It is perhaps immaterial whether these are "real" or major species, or minor ones, but since many modern segregates are mere ecads or herbarium myths, conversion is assumed to occur only when long accepted species are transformed. Such are the four species of *Mertensia*, for example, which have been recognized for a hundred years or more, having been named by Linne, De Candolle and Don; in recent times these have been split into more than a score of segregates. The adaptations, convergence

and morphological conversion of the original species of *Mertensia* and of many similar lineons in the experimental gardens have already been discussed to some extent (Plates 56, 57), but the behavior of composites and grasses presents aspects of special significance and will be considered more in detail.

**Composites.**—Of all the groups of flowering plants, the composites and grasses are by far the most satisfactory for phylogenetic studies. This is due largely to a new and complex structure, the head or spikelet, which has furnished occasion for a renewed evolutionary advance. Because of the recent and far-reaching differentiation, the comparative method attains its greatest success in these two groups.

In organizing the experimental attack, strategic genera have been selected for morphogenic manipulation as may be illustrated in the case of *Gaillardia*. The setose receptacle of this genus at once suggests that it is the connecting link between the paleaceous receptacle of the *Helianthiae* and the naked one of the *Heleniae*, this difference being the only important one between the two closely related tribes. The conversion of the setae into herbaceous bracts by hypotrophic induction, leaves little doubt of the origin of *Gaillardia*, and hence of the *Heleniae*, from the sunflowers, and at the same time indicates the essential sequence of the evolution of the receptacular bracts. Further evidence of the primitive nature of these two tribes is afforded by the development of the disk-florets in the axils of the bracts of the involucre, an ancestral condition no longer found in normal composites.

Much light has been thrown upon the evolution of the corolla and its phyletic significance by the development of the 5-toothed corolla of *Cichorieae* from the disk-florets of *Helianthus*, as well as the total suppression of the limb of the ligulate floret in *Agoseris*. The most significant modifications obtained, have been the conversion of the capillary pappus of the latter into a paleaceous one, clearly indicating that the latter is primitive, and the transformation of the corolla into setae, which points to the origin of pappus from calyx.

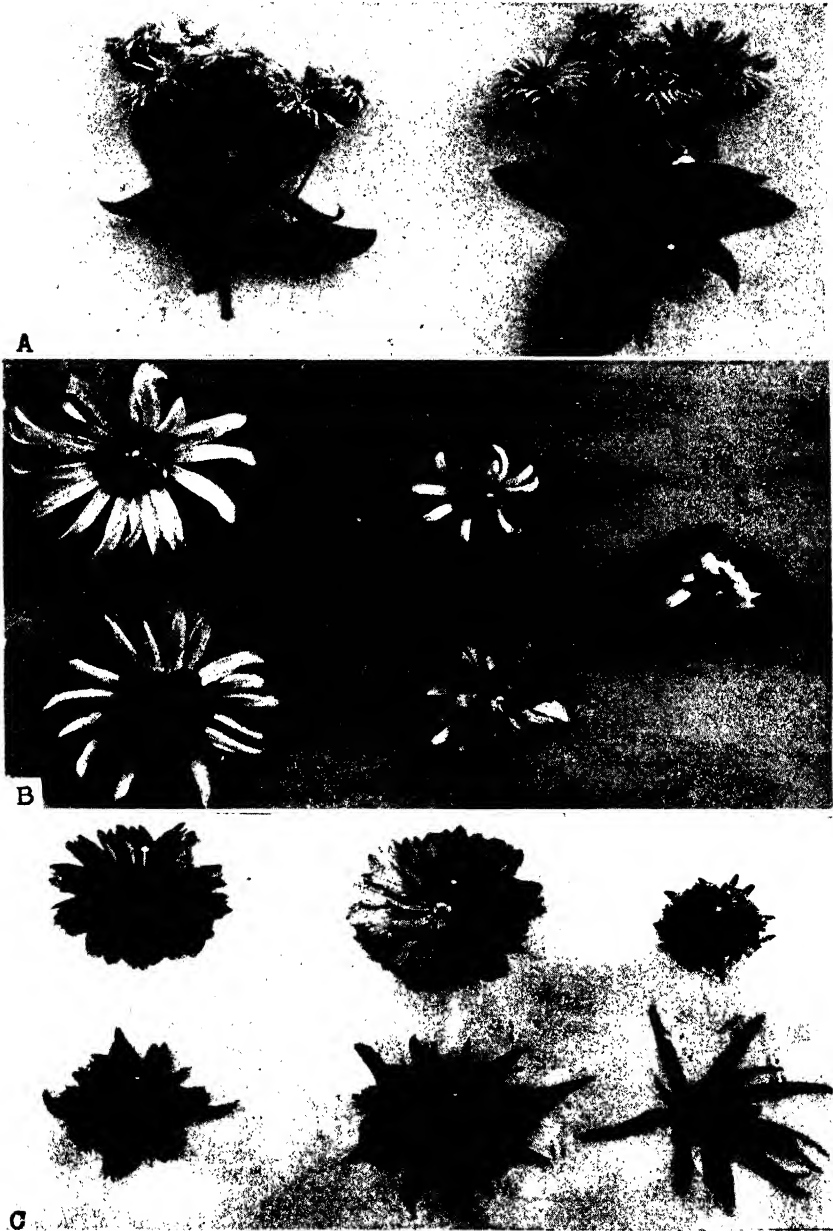
Transplants in the experimental gardens have undergone various modifications of differing kind and degree, from mere adaptations to changed habitats, to convergence and conversion between closely related species. During one of the driest years at the Alpine Laboratory, modifications were general in the way of reduced stature, size of flowers and heads, length of rays, number of disk and ray-florets, etc: The ex-

planation of the reduction of involucral and receptacular bracts, is competition—the latter merely carrying further the suppression typical of all bracts. When glucose is added or the number of bracts drawing in the food supply, reduced, they again revert to leaves, i.e. *Gaillardia*, *Dahlia*, and *Helianthus*. This also explains why marginal flowers are typically rayed and why disk-flowers appear in the bract axils of *Gaillardia*.

Other attempts to modify the criteria for species and sections have been unusually successful. In several composites, such as *Verbesina*, *Venegasia*, *Haplopappus*, *Erigeron* and *Actinella*, the involucral bracts may be transformed into foliaceous ones, often of great length, especially by shade in nature and under control (Plate 78). The typical glands of *Madia elegans* disappear under the influence of 4% shade, while the number of florets of *Solidago virgaurea multiradiata* has been decreased to a fourth of the normal, and conversely has been increased under optimum conditions for *Artemisia pattersoni* from 150 to 500. Moreover, after 5 years subjection to 5% light in the spruce climax, the latter species has become indistinguishable from *scopulorum*, which is evidently the ancestral type (Plate 79A).

A series of reciprocal transplants of the polymorphic *Artemisia vulgaris* offers results of value in applying the transplant method to taxonomy. Two varieties of this genus, which are commonly accepted as species are represented in the vicinity of the Plains Station by *ludoviciana* in which the leaves are only sparsely pubescent above, and *gnaphalodes* which has foliage densely white-tomentose on both sides. After 3 years of exchange of habitats, the plants of *ludoviciana* greatly increased the hairiness of the upper surface, and resembled *gnaphalodes*, but the latter had undergone little change. The taxonomic value of this lies, not only in the demonstrated change of one form into another, but especially in the fact that the tomentum is shown to be more easily acquired than lost. Moreover the results indicate that *ludoviciana* is the primitive form and *gnaphalodes* the derived one, and suggest that this may be true of other forms of *Artemisia*.

Of other paired or closely related species, *Actinella lanata* has shown definite convergence towards *acaulis*; the subalpine *Erigeron salsuginosus* has apparently changed into the parental *uniflorus* when transferred into the alpine garden, and the behavior of *glabellus* and *macranthus* as reciprocal sun and shade transplants has already been noted (Plates 58,59). Similar conversions in both directions have also



Involucre Overdeveloped in Shade.

A. *Erigeron macranthus*.

B. *Venegasia Carpesioides*: Upper row: Front views of 1. Normal sun form; 2 and 3, Shade forms; Lower row: 1. Bracts on sun form; 2. Bracts of shade form.

C. *Verbesina encelioides*: Upper row: Normal heads and bracts of sun forms; Lower row: heads with overdeveloped involucre grown in shade.

occurred in *Senecio cernuus* of montane forest shade and *bigelovi* in moist-sun at the same altitude, and *Helianthella quinquenervis* has converged toward *parryi* and finally become morphologically identical (Plate 80).

**Solidago Phylad.**—In the *Solidago* phylad, the ancestral species is represented by the circumpolar *virgaurea*, and *multiradiata* and *humulus* with their segregates are regarded as subspecies, as Gray saw them; *spectabilis* and probably *speciosa* also seem to be direct derivatives. *Solidago missouriensis* differs in triple-lobed leaves which can be readily traced to the form *lateralis*, while *serotina* appears a fairly fixed mesophytic partner in the phylad. Of the California species, *elongata* seems identical with *nemoralis*, and *spathulata* with *missouriensis* stock, while *californica* may approach *canadensis* (Plate 62).

In the transplant gardens, *Solidago speciosa*, *virgaurea* and *missouriensis* all exhibit the ease with which inflorescence characters can be changed, and thus indicate phylad lines across the sections. Conversions have taken place between *multiradiata* and *missouriensis*, while the latter and *serotina* have converged to the point of overlapping, and the alpine variety, *nana*, has changed to *humulus* by montane shade (Plate 79B). In order to insure that the results are not complicated by natural hybrids, an increasing number of species have been selfed, many of them to the fourth generation, and attempts at crossing have been made in not a few.

**Senecio Phylad.**—An excellent example of combined climatic and edaphic evolution is found in *Senecio aureus*. In the dry gravel slides of the montane region, this becomes *fendleri* and in the forest shade it is represented by the nodding *cernuus*. From the latter has sprung *bigelovi* of moist sunny places, with much larger heads, as well as a similar species, *amplectens* in the subalpine forest. In the alpine tundra, *aureus* becomes *croceus* which appears to be the ancestor of *fremonti* in moist shady rock-clefts, and of *taraxacoides* in dry gravel-slides. The latter is a dwarf with a single large nodding head which has been converted by means of shade into the probably ancestral *amplectens* in the adjacent spruce forest, the deepest shade producing rayless forms (Plate 81).

When transplanted to the montane forest and grown under watered conditions, *taraxacoides* has developed into a form scarcely distinguishable from *fendleri*. This has involved the elongation of the



Conversion of Alpines by Montane Shade.

- A. *Artemisia scopulorum* to *pattersonii*: 1. Typical alpine form of *scopulorum*; 2. Conversion form in montane shade; 3. Control *pattersonii* at 8,000 feet.  
 B. *Solidago nana* to *humilis*: 1. Typical *humilis*; 2. Converted *nana* in lath-house at 8,000 feet.



Convergence and Conversion.

A. *Senecio bigelovi* converging into *cernuus*.

B. *Helianthella quinquenervis* (1-3), passing into *parryi* (1-5).

stem from 2 cm. to 12 cm., the change from fleshy to thin leaves, the substitution of several erect heads for a single nodding one twice the size, the reduction of the rays from 13-15 to 7-8 and of their length from 14-20 to 7-8 mm. (Plate 82C). *Senecio croceus* has lengthened even more in similar situations, with corresponding modifications of the inflorescence, head and leaves (Plate 83).

**Grasses.**—The preceding changes lend support to the thesis that evolution is essentially a continuing process and that new forms may be produced more or less at will within the limits of a species as well as beyond, to close the gaps between related ones or to reintegrate the countless minor species of descriptive botany. As would be expected, the conversion of one genus into another, morphologically at least, is much more difficult than with species, but it is far from impossible. It is simplest in composites and grasses where the criterion is often single and technical, and responsive in some degree to the direct action of physical factors. As already indicated for the composites, the nature of the pappus may be altered to combine or separate related genera. Similarly, among the grasses, the technical difference of one spikelet at a joint as in *Agropyrum* and 2 in *Elymus* may be reciprocally modified in several species of each genus.

A complete series of modifications has been obtained with *Koeleria cristata* under four different habitats. In the watered sun-garden, the spikelets developed 3 fertile flowers; the native sun-form with rainfall alone, bore 2 fertile and 1 vestigial floret; the half-shade lath-house produced 2-flowered spikelets, while drouth plants were reduced to 1 flower with a vestige.

In *Trisetum spicatum*, the number of florets in the spikelets was shifted from 3 in the normal form to 4 in the sun-moist garden, and to 2 in the lath-house, while the related *montanum* of the spruce forest was converted in the sun, into morphological *spicatum*, its probable ancestor. The spikelet of *Bouteloua gracilis* was much modified in a light intensity of 12% in the Plains Garden, the 2 inflated sterile florets and tufts of basal hairs being reduced to the point of disappearance. As a result of renewed blooming in mid-winter in California, *curtipendula* was converted into *uniflora*. Here also, *Sporobolus airoides* apparently became changed to *wrightii* after 2 years of excess rainfall in the dunes.

Twelve percent of shade seems to have been responsible for shortening the spikelet and lengthening the rudiment in *Calamagrostis pur-*





*Senecio taraxacoides.*

A. Alpine dwarf in native habitat at 12,000 feet.

B. Conversion to *amplectens* in montane shade at 8,000 feet.

*purascens* so that they became equal instead of the latter being half as long, while drouth conditions diminished the spikelet by half and all but eliminated the rudiment. Shade has also decreased the spikelets in *Elymus canadensis* from 3-4 to 2 at a joint, the glumes narrowing to subulate. With *ambiguus*, the number was reduced from 2 to 1 by shade and raised to 3 by optimum water-content.

Timely rains in the Pikes Peak region brought forth a larger number of modifications than has been the case in the several dry years that preceded. Again the majority of the morphological conversions have concerned the grasses. The most signal success in producing an exact duplicate of an existing species from its assumed ancestor has been the conversion of *Phleum pratense* into *alpinum* by means of the water-transect. An ecological study of these, made it probable that all the distinctive features of the latter were due to water rather than to altitude directly. Hence *pratense* was transplanted into several stages of the water-transect with the result that it became identical with *alpinum*, and the following season the reciprocal conversion took place. At one stage in the process, the cylindric spikes of *pratensis* appeared on one plant of *alpinum* along with the globose heads of the species.

In the case of *Aira (Deschampsia) caespitosa*, flooding in the wet montane garden under protracted drouth, resulted in progressive vivipary; in many spikelets only the terminal floret was modified, the stamens and pistil disappearing and the scales turning green. In the next stage, 2 florets became virescent, the leaf-like scales developing ligules, and in the final case all three were more or less changed, to the point where rootlets were readily formed at the base.

Most of the genera of grasses under investigation have given one to several conversions of linneons and still more of subspecies. Chief among these are *Agropyrum*, *Elymus*, *Poa*, *Festuca*, *Bromus*, *Eragrostis*, *Melica* and *Stipa* (Plates 84-85). In addition to the experiments planned for the definite purpose of revealing phylogenetic relationships, practically every study in adaptation and fixation, as well as those of morphogeny, possesses phyetic value. In more than one case where the ancestral form was not even suspected, transplant experiments have disclosed clear evidence of origin and relationship. A striking example of this is the case of the peculiar alpine *Agropyrum scribneri*. Transferred to the shade in the montane zone, this underwent marked changes approaching closely the montane species *caninum*. This indicated that their areas should be somewhere in contact, and persistent search re-



Adaptations of *Senecio*.

- A. *Senecio fremonti* in alpine rock-cleft.  
 B. 1 and 2. Nodding and erect stems of *S. taraxacoides*; 3. and 4. Nodding and erect stems of *S. fremonti*.  
 C. Conversion of *taraxacoides* to *fendleri* in montane shade. 1 and 2. Native alpine dwarfs; 3. Conversion form at 8,000 feet.



A



B

*Senecio croceus.*

A. Alpine dwarf in native habitat at 12,000 feet.

B. 1. Alpine dwarf in sun at 12,000 feet; 2 and 3. Ecads of alpine native in degrees of shade at 8,000 feet.

sulted in the discovery of a small group of *scribneri* in the montane zone along a line of cold-air drainage, and of *caninum* on a warm slope at the lower edge of the alpine meadow.

**Festuca Phylad.**—*Ovina* is taken as the ancestral species, with *scabrella-thurberi* as high mountain, *brachyphylla* as alpine, *scabrella* boreal circumpolar, *viridula* local or regional, *rubra* as moist land and *occidentalis* in shade. These all grade completely into next of kin and are convertible by ecial pressure — leaves and awns changing to correspond and the decumbent stems equally modifiable. All can be grown in both the experimental gardens in California and the transplant gardens in Colorado, and in the reverse habitats without essential elimination.

**Agropyrum-Elymus.**—The technical difference between these two genera is that of 1 spikelet at a joint in *Agropyrum* and 2 in *Elymus*. This has been reciprocally modified in several species of each genus, and in addition, a new form-genus of *Elymus* has originated apparently by mutation, following the forest fire at the Alpine Laboratory in 1917.

A normal though luxuriant bunch of *Elymus* which had been under observation earlier, developed 3-4 spikelets with long pedicels at each joint, instead of 1-2 sessile spikelets. The pedicels were 10-15 mm. long in 1918 and widely spreading, giving the appearance of a narrow panicle. In 1920, the lateral spikelets had become short-stalked, while the two central still had long stalks. The spikelets were slender and terete instead of flattened, and the number of sterile florets much greater than in the normal ones.

The genus *Agropyrum* is usually divided into two sections in the manuals on the basis of the rhizome, which is highly modifiable, as has been indicated by results in the experimental gardens. The sod-forming species of the *smithi* group belongs to the *repens* stock which is chiefly Eurasian. They have a preference for high water-contents and hence characterize flat hard-lands on the one hand and dune soils on the other; this tendency is best exemplified by *repens*. By contrast the bunch-formers thrive in intermediate soils and are for the most part boreal to subalpine or correspondingly circumpolar and hence montane.

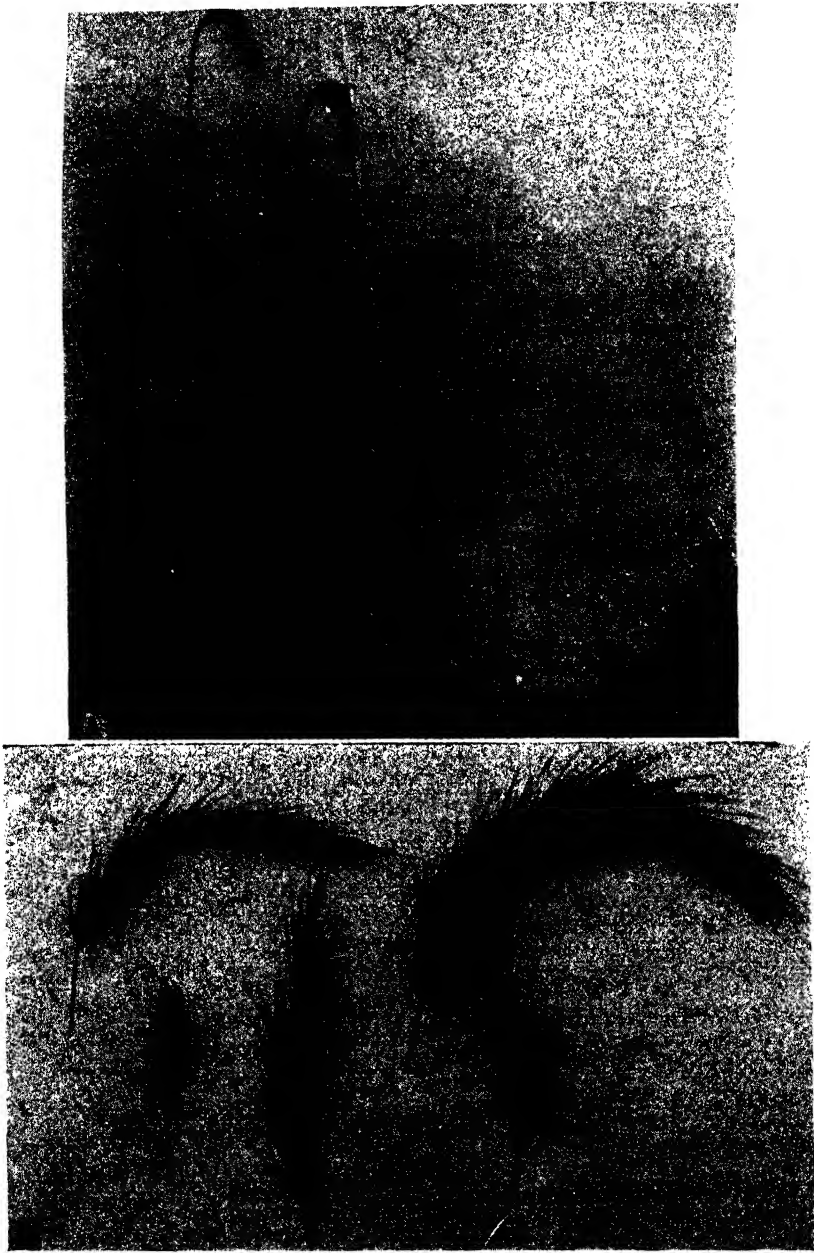
The wheat-grasses are mostly subclimax in nature; the major climax dominants are *smithi* and *pauciflorum* in the mixed prairie, and *spicatum* and *inerme* in the Palouse prairie. All are mid-grasses in terms of life-forms, though in dry sites or during drouth they become

more or less dwarfed. With rare exceptions, they are very hardy, respond readily to transplanting and cloning and are among the best for experimental purposes.

The question of the fixity of the sod and bunch habits as represented respectively by *Agropyrum* and *Elymus* has found an answer in nature, owing to the pressure of drouth, as well as in cultures. In the Plains Garden, for example, the rhizomatous *Agropyrum smithi* has formed bunches of as many as 14 culms, while the montane *Elymus ambiguus* has become a sod-former, producing rootstocks 4-5 inches long. Both of these modifications are in harmony with changed water-relations and are obviously produced by them.

**Stipa Phylads.**—The two major phylads of *Stipa* have been reconstructed experimentally, rendering it possible to trace the parallel evolution of species and climax associations around the circumpolar region and through the Western Hemisphere. A single species under two names, *capillata* and *comata*, extends across Eurasia and North America; as climates have differentiated, it has become adapted to them and each species thus produced has become the characteristic dominant of a new division of the climax. A second phylad, also under two names, *sibirica* and *viridula*, is likewise circumpolar but it is more northerly with higher water requirements. Hence its derivatives incline to be seral in nature and are more readily converted, both in nature and under experiment.

Four or five generally accepted species of *Stipa*, namely *viridula*, *vaseyi*, *lettermanni*, *columbiana* and *minor*, have been variously modified to overlap or duplicate each other, indicating that the last four are recent derivatives of *viridula*, and are to be treated as subspecies of it. This assumption is confirmed by their respective habitats. Conversions have also been made repeatedly within the series *capillata-comata-spartea*, while the southern species, such as *leucotricha-pulchra-eminens*, that do not survive Colorado winters, have been subjected to modification at Santa Barbara, where their conversions have been duplicated also. Even more significant, perhaps, than these controlled experiments has been the natural conversion of *comata* into *spartea* along the sandy escarpment of the Painted Desert. These have always been regarded as distinct species, but the accumulated evidence supports the view that the latter is a mesic variety of the former, representing it as a eudominant in the moister true prairie.



Natural Ecads of *Elymus canadensis* at 8,000 feet.

- A. 1. Sun-moist; 2. Sun-gravel; 3. Sun intermediate; 4. Competition with Blue Grass; 5. Sun-dry, gravel; 6. 20% sunlight.
- B. 1. Sun-moist; 2. Sun-wet; 3. Full shade; 4. Sun-moist, gravel;  
5. Sun-dry, gravel.



Ecads at 8,000 feet.

- A. *Agropyrum scribneri*: 1. Sun-moist; 2. Sun-wet (many compound spikes; 3. Lath-house (longest leaves).
- B. *Bromus purgans*: 1. Sun-dry; 2. Sun, hard soil; 3. Loose gravel; 4. Moist half-shade; 5. Dry full shade.



NOTE: TEXT-FIGURES OF GRASSES, FOLLOW CHAPTER XI,  
PAGES 262—272.

## CHAPTER XI

### SUMMARY AND CONCLUSIONS

More than four decades ago the first transplants were made on Pikes Peak for the purpose of throwing light upon the factors that produce change in plants. This region had been visited in 1896 in the course of a grazing reconnoissance for the Department of Agriculture, and the unique opportunities for experimental work in nature were then recognized. The chief of these was a range of climate and vegetation from temperate to arctic in a distance of seven miles, a situation found nowhere else on the North American continent, if indeed anywhere else in the world. With this went a great diversity of habitats, the almost complete protection afforded by water and forest reserves, and the ease of access provided by well-kept trails and, most important of all, the presence of a cog railway from the plains at the base of the Peak to alpine tundra at the summit.

Probably the earliest transplanters were the Neolithic lake-dwellers of Switzerland, who left an unwritten record of a score or more of species that they cultivated. However, the first suggestion of the transplant method is to be found in Bacon's proposal in 1635 that marsh herbs be planted on the tops of hills and dry plants in wet places. The initial attempt to do this was that of Naegeli more than two centuries later. However, he reversed the suggestion and brought alpine plants down to the botanic garden at Munich, but since the results were disappointing, he went no further. The earliest successful endeavor to use the method was made by Bonnier, first in 1884, but chiefly in 1887-89. He recognized the importance of using divisions of an individual plant and utilizing the same soil in order to avoid local effects. The accuracy of his results has been proven by later experiments, as well as his conclusion that plants transferred to alpine stations become identical with native forms often treated as valid species. His studies served as a stimulus for the work started on Pikes Peak in 1901. This was expanded in 1918 by the exchange of plants between California, Arizona and Colorado and the installation of a companion series of transplant gardens extending from the coast into the Sierras under Dr. Harvey M. Hall. About the same time, transplant gardens were

established in several climatic and edaphic sites from eastern Nebraska to Colorado, and ten years later control gardens for producing adaptations were organized at Santa Barbara, in which wandering and stable dunes were included. MacDougal had initiated a desert, mountain and coastal project at Tucson and Carmel as early as 1906, and recently the British Ecological Society has inaugurated edaphic studies based primarily upon soil.

The ruling principle of dynamic ecology is change—in both the organism and the community. This process has been the primary objective of the present studies, in the hope of discovering the various types and their relation to the environment. The many devices employed for producing modification are practically all variations of three primary methods, namely, transferring the plant to a different habitat, modifying the habitat or one controlling factor, and disturbing the nutritional balance in the plant body. The technique of breeding has also been utilized to obtain selfed seed, to test the constitution of native species in some degree and to determine whether the units employed would hybridize.

It was naturally foreseen that the question of the relative parts played by environment and heredity would be concerned in the results, as well as that of the transmission of acquired characters, though it was not anticipated that the evidence would yield a novel answer. An additional point of great interest was whether the outcome would support the earlier or later views of Darwin. A number of critics have attacked the major conclusion of the "Origin of Species" with much justice and equal success. But few of them seem to have known that they were demolishing a view that Darwin had begun to doubt three years after the publication of the "Origin," and had greatly modified if not forsaken by the time that "Variation of Plants and Animals under Domestication" had appeared. In 1876, he was writing to Wagner, the advocate of origin by isolation, "In my opinion the greatest error that I have committed has been not allowing sufficient weight to the direct action of the environment, i.e., food, climate, etc. independently of natural selection." "When I wrote the 'Origin' and for some years afterwards, I could find little good evidence of the direct action of the environment; now there is a large body of evidence."

**Methods and Materials:**—Little more can be said here than to mention the five major gardens, three of which are located in Colorado:

one at the base of Pikes Peak at 6,000 ft., another on the slopes at 8,000 ft., and the third near the summit at 12,000 ft. The other two lie respectively at the foot of the Santa Ynez mountains at Santa Barbara, California, and in a small dune area along the shore, eleven miles north. Each climatic garden comprises several edaphic ones in which one factor is controlled, as in the series of six light intensities, and four degrees of water-content in the main garden at Santa Barbara. In the endeavor to disturb the nutritional relations within the individual plant, a wide variety of methods has been invoked, but practically all deal with the increase or decrease of food to a particular organ or part, or with an upset of the bio-chemical balance.

The materials employed have comprised native species for the most part, though the vigor of many garden varieties has given them the preference in some control series. Five different floras have been drawn upon to an extent designed to be representative of the various herb life-forms, with a small number of shrubs. These are the prairies of the Middle West, the coniferous forests of the Rocky Mountains, the alpine tundra, prairie and chaparral of southern California and the deciduous forest of the East. Each of these has contributed from one to two hundred species for more or less extensive experiment, and an additional two to three hundred have been drawn from the botanic gardens of other countries and from cultivation. In the transplant gardens, many thousand individuals of the more important natives have been installed, while in the control series most of the species have been replicated for three to five seasons.

**Genetic Tests:**—These have been directed mostly to the question of the possible hybrid constitution of the native species utilized. This has been done primarily to obtain a fair degree of uniformity among the individual plants employed, but it has also given some evidence as to the number of natural hybrids in the floras concerned. In addition, it has revealed a number of self-sterile species. The regular procedure has been to carry the analysis through three generations, although some species have been selfed four or five times. The total number of species dealt with thus far is 310, of which 19 have yielded no seed and are probably to be regarded as self-sterile.

Crossing has been employed in a much smaller number of species, chiefly with reference to its supposed value in distinguishing between species and forms of lesser rank. It has been uniformly successful in

the case of dominant and recessive criteria, and these of course have been readily segregated by selfing. But crosses between groups with the character of Linnean species have failed in all cases tried, and this has likewise been true of sub-species in such plants as *Oenothera biennis*, in which it was supposed that hybridization would be a general result. Altogether several thousand individuals have been selfed, but in none of the 292 species concerned was there any evidence of segregation or of any departure beyond the range of variation in the parent material.

**Adaptation:**—In the dynamic sense, adaptation is the process by which plants are molded by their environment, leaving aside the question as to whether hybridization and mutation may not belong largely in the same category. For the sake of clearness, the results secured may well be considered under the following headings: (1) action of such direct factors as water, light and nutrients, (2) readjustments for correlation in the individual, (3) ecads and ecotypes, (4) convergence and conversion. However, it should be realized that these are only different degrees or manifestations of a single complex process of change.

Adaptation is considered to be the complete response of plant and species—i.e., the species-individual or spicient—to the habitat complex, or more often to the dominant factor in it. It thus comprises the entire sequence from factor to function, form and phylogeny. For a full understanding, it is essential to measure factors and functions, as well as the resulting structures and criteria. For factors, this is partly accomplished by the various physical instruments, but in order to evaluate these causes in terms of plant effects, batteries of phytometers are indispensable. They likewise have the further value of serving as experimental proxies for the native species, which usually take much less kindly to control. Some of these do lend themselves more or less readily to functional measurements and hence help to interpret the structural changes of those species that are less complaisant.

About 150 species have been grown in the several factor series; the majority of these range through 18 control habitats, namely, four degrees of water and nutrients, six of light, three soils, three lengths-of-day, and two dune types. A score or so have been included in as many as six to eight seasonal replications, in order to provide a back-

ground of comparison. In addition, a number have been subjected to four degrees of competition: 4, 16, 64, 128 or 256, in a square meter. Out of the great mass of details have emerged a number of working hypotheses. The most important of these is concerned with the view of Kämmerling and some other geneticists that adaptation is merely the selection of genetic strains capable of living in the habitats employed. However, in the large majority of cases, virtually all the individuals survive, 25, 50 or 100, in accordance with the number planted. When they do succumb, as in 3% shade, or on mobile dunes, they usually disappear completely. Even more significant is the fact that when losses occur, they are as great or greater for controls, and this is equally true of divisions and of selfed progenies. In short, the experimental evidence thus far secured indicates that adaptation affects all the individuals and in the same manner, and that it is a universal process to which all species are subject in varying degree. Each direct factor brings it about in accordance with intensity and duration and each leaves a more or less characteristic impress as a consequence.

More striking still is the behavior of one individual under different intensities of a factor. This is best seen in the case of light, when half the plant is grown in sun and the other half in shade, but it may also be demonstrated by changing conditions for the whole plant in the course of the season's growth, or by changing the habitat of a perennial from one year to the next. This is readily done in position, but is commonly achieved by transplanting, as in the series of altitude gardens.

**Correlation and Manipulation:**—Correlation in the plant body is primarily a condition of balanced competition between the various organs, parts and tissues. The competition for food as energy, and for water as the agent of growth and modification, seems to be determined by demand and by access. The main stem has the advantage over lateral shoots, the basal flowers of a raceme over the upper, the lower florets of a *Festuca* spikelet over the upper, and the upper of *Panicum* over the lower, paired stamens over unpaired, and so forth. This is well understood theoretically, but it has received too little attention practically.

The technique of manipulating plants and organs to produce changes, rests squarely upon the kind and amount of competition between the correlated parts. The balance is extraordinarily delicate, a

few days of fog and reduced photosynthesis being sufficient to change the number plan in *Verbascum* flowers from 6 or 7 to 4 or 5. The entire plant may be manipulated by sharp changes in water, nutrients, light or temperature, or the access of food to any organ or part, or its utilization there may be modified in a large number of simple ways. Thus, dwarf albino flowers may be produced by bending stem or peduncle sharply or by severing certain bundles. Growing points, axes, lateral buds, etc. may be cut off, or flower-parts, particularly stamens, pistils, or their primordia, may be excised in varying degree. Attached glucose tubes with solutions of  $\frac{1}{2}$ -1% are employed for producing hypertrophy directly, while injections of dilute acids and bases, of enzymes and hormones, are made with a syringe.

Changes in physical factors modify the vegetative body directly, but as a rule they operate upon the reproductive parts only through the agency of nutrition, probably in the same manner as direct manipulation. Forms of energy, light and temperature, to say nothing of electric charges, x-rays and alpha and beta rays, may likewise act directly upon flower and fruit, but this appears to be rare at the intensities found in nature.

**Ecads and Ecotypes:**—It became evident rather early in the transplant studies that habitats are often not what they appear to be. This is best illustrated by altitude, where the alpine vegetation is characterized by marked dwarfing. It was thought at first that plants moved down from an altitude of 12,000 feet into montane or plains climates at 8,000 and 6,000, would respond by increased stature and related changes, as Bonnier found to be the case in Europe. In many species this did not happen, and it was soon discovered that dwarfing by drouth was nearly as possible in the mixed prairie as in the alpine tundra. Somewhat similar results have been obtained at Santa Barbara, where the rainless California summer is the critical factor. Furthermore, on the summit of Pikes Peak, dwarfing is largely confined to the climax areas, which are much the most extensive, whereas well-watered sites or disturbed soils within the area may yield plants tenfold taller. At the outset also, much faith was placed in reciprocal transplants, in natural habitats, as in the case of species paired in sun and shade or wet and dry, but they proved a disappointment and were abandoned.

The term ecad has been employed to designate forms that were

obviously produced by the particular environment, and experimental proof of this has been obtained in many cases. Some of them probably correspond to the biotypes of the geneticist, but this can be proved only by further transplant studies. A considerable number have been regarded as ecotypes by Turesson, who finds them to be fixed or stable forms. Some of these, like the dwarf form of *Campanula rotundifolia*, are common to America and Europe. It is possible, though hardly likely, that they are of different character on the two continents, and the more probable explanation is that they are neither completely fixed, nor wholly unstable. In short, they appear to vary widely in fixity in accordance with the parent species, or the kind of treatment.

This applies especially to the alpine ecads, some of which are derived from circumpolar arc-alpine stock and hence are relatively old, while others have come much more recently from temperate species of the region. The latter are more easily modified as a rule, though no alpine dwarf has proved entirely stubborn. By contrast with these, the species transplanted from the plains or montane climax, respond to the alpine climate by losing a half or more of their stature the first year after removal, and often exhibit further reduction during the next two or three years. Within each of the three climates, there are many edaphic ecads, natural and induced, nearly all of which are recent in origin and generally modifiable in a single season, although the intensity of change, or dosage, plays a large part.

When the dosage is moderate and the conditions for growth approximately optimum, modification is slow or slight, and the ecad appears to be an ecotype. A garden with these qualities is more or less neutral in action and is consequently not an adequate test of fixity. Thinking as he must in terms of dynamics, the ecologist has come to the point of indicating fixity for each character in terms of the factor dosage it can withstand. This has the further advantage of permitting the arrangement of criteria in a series corresponding roughly to the units: form, variety, sub-species, and species, and in some cases, genus.

**Convergence and Conversion:**—The Pikes Peak region is peculiarly rich in closely related pairs or groups of species, partly because of the number of climax floras represented and partly because of highly broken topography. This is fortunately true of the traditional species or linneons, and these have afforded a unique opportunity for retracing lines of relationship and probable evolution as a



basis for the experimental attack upon the problem. In nearly all cases, the paired species occupy opposite types of habitats, thus, *Eri-geron glabellus* prefers the shade of spruce forests, *macranthus*, the full sun of openings and meadows. Each bears the full imprint of the controlling factor of its habitat, but between them in both position and form lie a number of minor species, most of which have been given binomial names. *Geranium richardsoni* haunts moist shade along brooks, while its relative *caespitosum*, has developed in harmony with the factors of hot gravel slopes. Among the groups of species, the circumpolar *Mertensia sibirica* follows brooks and wet meadows from the montane zone into the lower alpine tundra where it meets *alpina*, a typical endemic of high peaks. At the lower altitudes, *sibirica* lies close to *pratensis* in the forest, and *lanceolata* on warm slopes. Of the grass groups, *Agropyrum*, *Elymus*, *Festuca* and *Stipa* have been especially well adapted to the technique of conversion and have yielded results in large number.

In many instances, the conversion of sections or of genera presents little more difficulty than that of species, especially in the great groups characterized by relatively recent and rapid evolution, namely grasses and composites. A large number of these are distinguished by a single technical character, such as the presence or absence of rhizomes, awns, pappus, rays, double pappus, triple-veined leaves, number of flowers in a spikelet, position of the awn, presence or absence of chaff, forms of involucre bracts, annual and perennial habit, diclinism, etc. Some of these show a certain amount of variation in nature, and all of them have been modified in experimental cultures. Technically, *Agropyrum* and *Elymus* are separated on the number of spikelets at each joint of the rachis, but *Agropyrum* often develops two, and *Elymus* is reduced to one. When generic limits rest upon the disposition of stamens and pistils, conversion can frequently be brought about by the suppression of one or the other.

**Species and Phylads.**—The ecologist who has had the good fortune to work in the field during the twelve-month year, is peculiarly handicapped by species as they appear in manuals and monographs. He can neither make effective use of them, nor can he break away from them entirely. He recognizes that this is much less the fault of taxonomists in general than it is of botanical custom, in America especially. Our national fondness for hurry, rules out the trinomial, and

hence the binomial too often comes to stand for anything distinguishable, irrespective of its rank or origin. There is an occasional tendency in the other direction, which may be illustrated by the genus *Mertensia*. For the mountain region, the 5 species of Gray become in Rydberg's manual, 48 species in sections, if the binomial is to be taken as an index. Nelson recognizes 14 species and 10 varieties, while the recent monograph by Williams contains 15 species and 16 varieties. In spite of this, it will be a long time before taxonomy in this country employs the trinomial as a matter of course, after the fashion of ornithologists.

In coming to recognize that change is everywhere as active in species as in communities, the ecologist has been obliged to think in terms of dynamic units. It is just as imperative to turn away from the heterogeneous and static species as it has been to forsake the formation of Warming or the association of the plant sociologists. Such a unit must comprise a definite and measurable section of the stream of evolution and for convenience sake it must have a name, which no one is expected to use until he has a use for it. This dynamic unit has been termed a phylad, from *phylum*; it differs from the species, and especially the minor species, in being a *continuum* in which the many parts are subordinate to the whole. The familiar names of the component species appear in it, but merely as knots in a thread. One of the two major tasks of dynamic ecology during the past forty years has been the reconstruction of phylads by means of field study of variation and adaptation, and the experimental production of intermediates and conversions. Practically all the genera utilized in the transplant gardens, exhibit phylads, and these have permitted a long look backward into the world-wide migration and origin of species.

**Climatic Cycles and Mass Migration.**—Modern ecology with its concept of the climax as the product of climate, and of the clisere as a succession of climaxes driven by climate, has done much to refashion paleo-botany, and in turn the new field of paleo-ecology has thrown a flood of light upon existing vegetation and floras. From this has emerged the basic principle that climatic cycles produce mass migrations as a consequence of which new species are evolved to form new floras. This concept replaces almost completely the earlier view that migration is largely a random affair of individuals and that existing species of plants have practically all evolved since the beginning of the Pleistocene. Species found in the tropics today extend as far back as

the Eocene it seems, and many temperate ones originated as early as the Oligocene or Miocene. From their homeland in Holarctica, the latter have spread out over the Old and New Worlds, and not a few have advanced far into the Southern Hemisphere. No genus illustrates this combined migration and evolution better than *Stipa*. It is perhaps without a peer in importance and extent, not only as to the number of species, sub-species and forms, but also as having a dominant role in climax associations the world over. As the most highly specialized of grasses, it has undergone rapid and comprehensive evolution which is reflected in the differentiation of grassland on all the continents. Originating in the circumpolar region of the Northern Hemisphere, it has been driven southward by climatic shifts; it has crossed the equator at times of high continental emergence and has spread out over Australia, Africa, and South America, far into Patagonia.

The extensive collections in the U. S. National Herbarium have been studied in detail with especial reference to the original stocks and their modification as they were dispersed throughout the globe by virtue of climatic compulsion. The major stocks are largely identical for Eurasia and North America, and several of these continue into South America with the evolution of a host of new forms. The African species are for the most part those of Europe or derivatives of them, while the Australian ones, though evidently derived from Asiatic ancestors, reflect a longer break in land connections. It seems probable that the line of continuous descent that is represented by *capillata* of Eurasia, *comata* of the Great Plains, *pulchra* of California, *leucotricha* and *mucronata* of Texas and Mexico, and *neesiana* of Central and South America, is unsurpassed as an example of evolutionary migration.

### CONCLUSIONS

As a consequence of the modification of about 200 genera and approximately four times that many species in the transplant and adaptation gardens, it is felt that the evidence warrants the following conclusions. Some of these are supported by a greater weight of evidence than others, and it is fully recognized that further extension and replication on a large scale are essential to a fair degree of finality.

- (1) Adaptation is a universal process, brought about by response to direct physical factors and expressed both in function and in form. For all the species employed, there is no evidence that it

arises through the selection of genetic strains or variations. This is indicated likewise by the different types of material, no species having yet been discovered in which the clones differ from the adult individuals in the response to the various factors.

- (2) Natural selection does not operate upon the forms produced by adaptation, since they are immediately in harmony with the environment that produces them.
- (3) Correlation, that is, competition within the plant body, seems to be the mechanism by which energy-changes in the vegetative body are transmitted to the reproductive organs.
- (4) Change is the primary process; fixation is consequent upon it. Since time and intensity of dosage appear to be the essence of fixation, the degree of the latter is most readily seen in the number of years necessary to modify a particular character, such as dwarfness, pubescence, shape of leaves, and the specific criteria drawn from flower and fruit.
- (5) The species of tradition, with their many minor segregates, are for the most part, sections of a continuous stream of evolution, known concretely as a phylad. Most species permit of a wide range of adaptation in accordance with a particular direct factor or a complex of two or more. They change their expression with the habitat, and the typical form, ecologically speaking, is that which occupies the most extensive area.
- (6) Climate directs the simultaneous evolution of climax and species, edaphic or seral habitats placing a secondary impress upon both.
- (7) Finally, the original assumption that research in adaptation is pre-eminently a field for cooperation between investigators of diverse training and outlook, has been increasingly verified by the experience of more than four decades. This is chiefly necessary for a well-rounded viewpoint and a comprehensive attack, but it is also indispensable to the manning of a problem with so many and so varied facets.

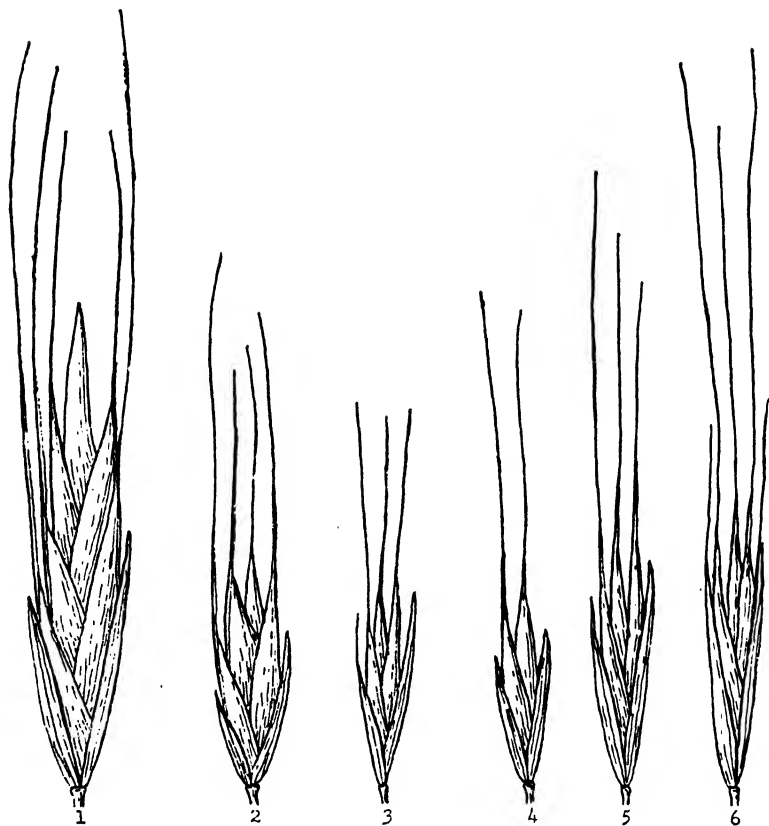


Fig. 1. *Agropyrum caninum* (x 2.6)

PLAINS: 1. Sun-Medium; 2. Half-Shade Medium; MONTANE:  
3. Half-day-Sun Dry; 4. Sun-Dry; 5. Sun-Medium; 6. Sun-Moist.

## AGROPYRUM CANINUM

<u>Criteria</u>	<u>Plains Climax</u>		<u>Montane Climax</u>
	<u>Sun-Medium</u>	<u>Half-Shade Medium</u>	<u>Half-Day-Sun Dry</u>
<u>Culm:</u>			
Ht-diam.	90cm x 2.5mm	77cm x 1.5mm	33-57cm x 1mm
<u>Leaf:</u>			
Number	3	5	4-5
Size	22cm x 6-7mm	23cm x 3mm	11-15cm x 2-4mm
Ligule	.5mm	.5mm	.5-1mm
<u>Spike:</u>			
Size	20-26cm x 5mm	11cm x 3mm	3-7.5cm x 2-5mm
<u>Spikelet:</u>			
Number	15	11	5-12
Size	20-25 x 5mm	9-12 x 3mm	9-11 x 1.5-2mm
Floret	6-7	3-4	2-3
<u>Glumes:</u>			
Size	10:11mm	7:8mm	6:7mm
Awns	1:2mm	2:2mm	3:4mm
Nerves	3:4-5	3:3	3:3
<u>Lemma:</u>			
Size	7.5, 8mm	6.5, 7mm	7, 8mm
Awn	15-20mm	10-15mm	10-9mm

<u>Criteria</u>	<u>Montane Climax</u>		
	<u>Sun-Dry</u>	<u>Sun-Medium</u>	<u>Sun-Moist</u>
<u>Culm:</u>			
Ht-diam.	61cm x 1mm	<u>Small Culm</u> 37cm x .8mm <u>Tall</u> 62cm x 1.5mm	93-101cm x 3mm
<u>Leaf:</u>			
Number	2-3	4	4
Size	10-13cm x 2mm	8-9cm x 7-8mm	10-11 x 1cm
Ligule	1mm	.5mm	.5mm
<u>Spike:</u>			
Size	9-14cm x 2-3mm	7cm x 1.5mm	15cm x 3-4mm
<u>Spikelet:</u>			
Number	8-11	13	20
Size	9-10 x 2mm	10-12 x 1.7mm	15 x 2mm
Floret	1-2	2-3	6
<u>Glumes:</u>			
Size	8:9mm	6:7mm	7:8mm
Awns	.5: .5mm	2:3mm	3:5mm
Nerves	3:5	3:5	4:5
<u>Lemma:</u>			
Size	8mm	7-8mm	8-9mm
Awn	16-20mm	14-16mm	12-22mm
			20-30mm

Note: In the tables of measurements for grasses, "Medium" refers to the amount of moisture; "Half-Shade" is the same as "Half-day Shade"; "Full-Shade" and "Deep-Shade" are the same; "Sun-Shade" refers to alternating sun and shade all day.

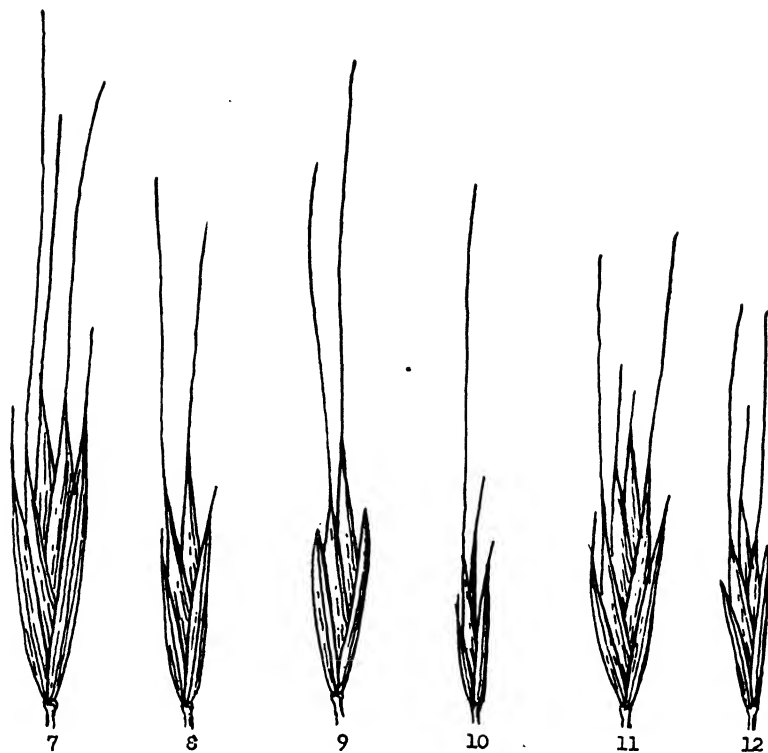


Fig. 2. *Agropyrum caninum* (x 2.6)  
MONTANE: 7. Half-Shade Medium; 8. Full-Shade Medium;  
9. Full-Shade Moist; 10. Deep-Shade Moist;  
ALPINE: 11. Moist-Season; 12. Dry-Season.

AGROPYRUM CANINUMMontane Climax

<u>Criteria</u>	<u>Half-Shade Medium</u>	<u>Full-Shade Medium</u>		<u>Full-Shade Moist</u>
<u>Culm:</u>		<u>Small Culm</u>		<u>Tall</u>
Ht-diam.	74-86cm x 2mm	43cm x .9mm	100cm x 1.6mm	98-125cm x 1-1.7mm
<u>Leaf:</u>				
Number	4-5	5	6	3-4
Size	20-26cm x 3-4mm	12cm x 2-3mm	17cm x 5-8mm	20-26cm x 2.5-4mm
Ligule	.7mm	.5mm	1mm	.6mm
<u>Spike:</u>				
Size	10cm x 4mm	1.5-2cm x 2mm	9-10cm x 3mm	7-20cm x 2-3mm
<u>Spikelet:</u>				
Number	15	2-4	18-24	10-15
Size	11-14 x 3mm	6-8 x 1.5mm	11 x 2.5mm	12-14 x 1.6-2mm
Floret	3	1-2	2-3	1-2
<u>Glumes:</u>				
Size	11.5:13.5 x 2mm	5:6mm	7:8mm	8:9mm
<u>Awns</u>	3:4mm	1:2mm	1.5:2mm	.3mm
<u>Nerves</u>	6:6	3:3	3:4	3:5
<u>Lemmas:</u>				
Size	11,10mm	7-8mm	8-9mm	9,7mm
<u>Aw</u>	23,18mm	12,10mm	14,12mm	16-25mm

Montane ClimaxAlpine Climax

<u>Criteria</u>	<u>Deep-Shade Moist</u>	<u>Moist -Season</u>	<u>Dry-Season</u>
<u>Culm:</u>			
Ht-diam.	59cm x 1mm	42-44cm x 2.5mm	28cm x 1.5mm
<u>Leaf:</u>			
Number	6	4	4
Size	16-17cm x 4-5mm	16cm x 4mm	8cm x 4mm
Ligule	.5mm	.5mm	.5mm
<u>Spike</u>			
Size	5cm x 2mm	10-12cm x 6-8mm	6.5-9cm x 5-6mm
<u>Spikelet:</u>			
Number	8	18-21	14-17
Size	8-9 x 1.4mm	12-13 x 3mm	9-10 x 2mm
Floret	2	3-5	1-3
<u>Glumes:</u>			
Size	4.5:5x1mm	7:8mm	6:7mm
<u>Awns</u>	2.5:4mm	1-2:2-3mm	.2:1.5mm
<u>Nerves</u>	2:3	3:5	3:4
<u>Lemmas:</u>			
Size	6-7mm	8,7.5:9,8mm	7,8mm
<u>Aw</u>	9-10mm	13-14mm	10-11mm



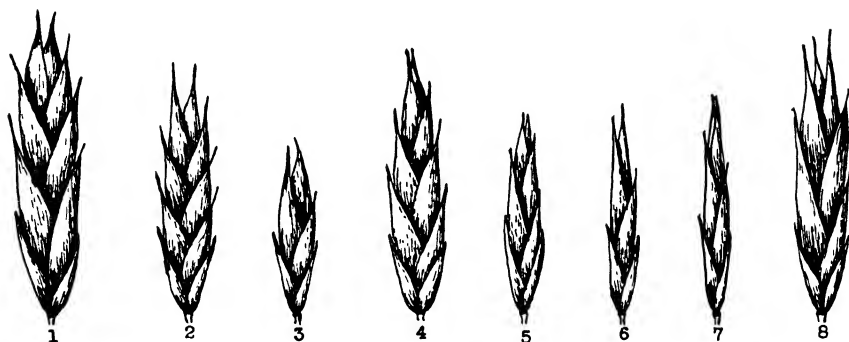


Fig. 3. *Bromus catharticus* (x 1.2)

1. Sun-Moist; 2. Half-Shade; 3. Full-Shade; 4. Sun-Medium;  
5. Sun-Dry; 6. Muck; 7. Competition Suppressed; 8. Competition Dominant.

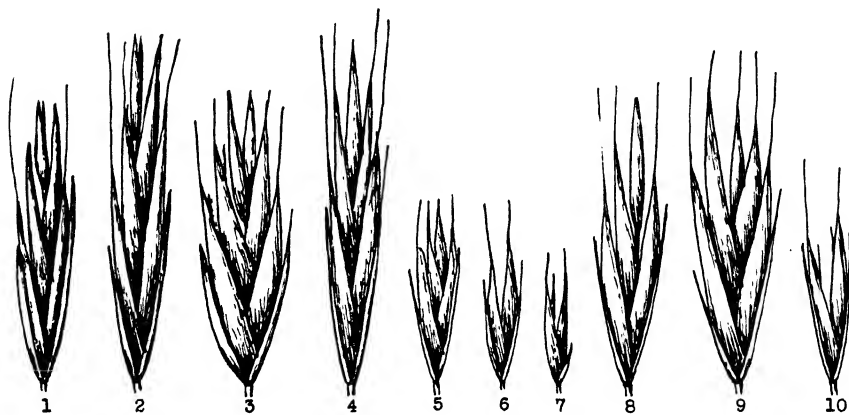


Fig. 4. *Elymus ambiguus* (x 2)

MONTANE: 1. South-Slope Medium; 2. South-Slope Moist; 3. North-Slope Moist; 4. Half-Day-Shade Moist; 5. Half-Shade Dry;  
6. Half-Shade Wet; 7. Full-Shade Dry; SUBALPINE: 8. Sun-Medium;  
ALPINE: 9 Sun-Medium; 10. Sun-Dry.

## ELYMUS AMBIGUUS

Criteria	<u>Plains Climax</u>		<u>Montane Climax</u>		
	<u>Sun-Medium</u>	<u>Half-Shade Moist</u>	<u>Sun-Dry</u>		
Culm:			Small	Plant	Tall
Ht-diam.	55-67cm x 2mm	78-91cm x 2mm	41-64cm x 1.5mm	110cm x 3.2mm	
Leaf:					
Number	3-4	3-4	3-4	4	
Size	21-28cm x 2.5-3mm	24-26cm x 3mm	16-18cm x 3-4mm	22cm x 8mm	
Ligule	.7mm	.5-.7mm	.1-.2mm	.2-.5mm	
Spike:	10-12.5cm x 12mm	9.5-12cm x 10mm	6.5-11cm x 5-9mm	11cm x 1cm	
Spikelet:					
Number	2(3)	1-2	1-2(4)	22	
Size	13-15 x 4-5mm	11-12 x 4mm	10-14 x 4mm	17-20 x 3-4mm	
Floret	3-4	2-3	3	5-6	
Glumes	10:11 x .5-.6mm	6:9 x .3mm	6:10 x .2mm	7:10 x .5mm	
Lemma	11-18mm	7-9mm	7-8mm	9.5-10mm	
Aw	1.5-2mm	2.8-4mm	4mm	3.5-4mm	

Criteria	<u>Montane Climax</u>			<u>Montane Climax</u>	
	<u>Sun-Medium</u>	<u>Sun-Moist</u>	<u>Half-Day-Sun Moist</u>		
Culm:					
Ht-diam.	Small 42-65cm x .7-1mm	Plant 91-109cm x 1-1.5mm	Tall 119cm x 1.8mm	142cm x 1.5mm	
Leaf:					
Number	4	4-5	3	4	
Size	8-18cm x 1-5mm	11-28cm x 4.5-8mm	10-12cm x 2mm	19-28cm x 6.5mm	
Ligule	.1-.2mm	.8-1mm	.5mm	.4mm	
Spike:	7-11cm x 3-4mm	12-14cm x 7-11mm	10cm x 4mm	14cm x 4mm	
Spikelet:					
Number	(1)2	(2)4	15	25	
Size	11-15 x 2-2.5mm	15-20 x 2.5-5mm	15-20 x 4mm	21 x 2.5-3mm	
Floret	2-3	5	3-4	5	
Glumes	6:11mm	10-15mm	6-7:8mm	10-10.6:9mm	
Lemma	8-10mm	9-10.5mm	9-10mm	12-13mm	
Aw	2-4.5mm	4-6mm	3-5mm	1-2mm	

Criteria	<u>Montane Climax</u>			
	<u>Sun-Wet</u>	<u>South-Slope Medium</u>	<u>South-Slope Moist</u>	<u>North-Slope Moist</u>
Culm:				
Ht-diam.	110cm x 3.5mm	80-90cm x 2mm	90-100cm x 1.5-2mm	75-85cm x 3.5-4mm
Leaf:				
Number	4	3	4	5
Size	33cm x 7mm	12-17cm x 6-7mm	23-29cm x 5-6mm	24-31cm x 8-9mm
Ligule	1-1.5mm	1mm	1mm	.5mm
Spike:	13cm x 10mm	9-11cm x 7-9mm	11-13cm x 4-5mm	10-11cm x 10mm
Spikelet:				
Number	31	(2)3-4	1-2(3)	3-4
Size	20-25cm x 4mm	14-19 x 3-4mm	19-21 x 3-4mm	18-23 x 4mm
Floret	6-7	4-5	4-6	4-6
Glumes	3:7-9mm	8:12mm	7:13mm	7:10-13mm
Lemma	10-11.5mm	9-10mm	10-11mm	13-15mm
Aw	2-5mm	2-7mm	3-6mm	2-5mm

ELYMUS AMBIGUUSMontane Climax

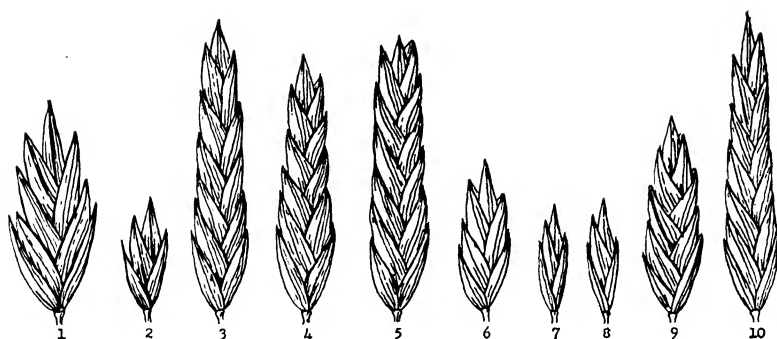
<u>Criteria</u>	<u>Half-Shade Dry</u>	<u>Half-Shade Medium</u>		<u>Half-Shade Wet</u>
<u>Culm:</u>		<u>Small</u>	<u>Plant</u>	<u>Tall</u>
Ht-diam.	31-37cm x 1.7mm	65cm x 1mm	121cm x 2mm	57cm x 1.5mm
<u>Leaf:</u>				
Number	3-4	4	5	4
Size	19-21cm x 3.5mm	21-30cm x 3mm	34-36cm x 6mm	8-10.5 x 2mm
Ligule	.3mm	.8mm	1mm	.1mm
Spike:	4.5-6cm x 5-7mm	7-8cm x 2mm	12-13cm x 4mm	6cm x 4mm
<u>Spikelet:</u>				
Number	1-2	1-2	1-2	1-(2)
Size	9-11 x 3mm	8-10 x 1.5-2.5mm	16 x 3mm	7 x 2-3mm
Floret	3	1-3	3	1-(2)
Glumes	7:9mm	5:7mm	8:10mm	7:8mm
Lemma	9mm	7.5-8mm	9-10mm	7-8mm
Awk	2-3mm	2-3mm	3-4mm	2-4mm

Montane Climax

<u>Criteria</u>	<u>Half-Day-Shade Moist</u>	<u>Half-Day-Shade Wet</u>	<u>Full-Shade Dry</u>	<u>Sun-Shade Moist</u>
<u>Culm:</u>				
Ht-diam.	58-60cm x 1.7mm	50-71cm x 1.8mm	57-58cm x 1.5mm	100-115cm x 3mm
<u>Leaf:</u>				
Number	3-4	3-6	3-4	3-4
Size	25-30cm x 3mm	18-26cm x 5mm	7-13cm x 3mm	30-45cm x 7mm
Ligule	1mm	.5mm	.3mm	1mm
Spike:	9.5-11cm x 7mm	10-11cm x 4mm	2-5cm x 2-3mm	11-13cm x 8mm
<u>Spikelet:</u>				
Number	(1)-2	1	1	2-3
Size	15-17 x 4mm	9-12 x 1-2mm	10-12 x 1-1.5mm	18-20 x 4-5mm
Floret	3-4	1-3	1-2	4-5
Glumes	8:10mm	5:7mm	0:0-5mm	6:10mm
Lemma	9-10mm	6mm	8-11mm	9-12mm
Awk	2-3mm	6mm	.5-2mm	1.5-3mm

Subalpine ClimaxAlpine Climax

<u>Criteria</u>	<u>Sun-Medium</u>	<u>Sun-Medium</u>	<u>Sun-Dry</u>
<u>Culm:</u>			
Ht-diam.	68-76cm x 1.5mm	34-45cm x 2.5mm	14-20cm x 1.3mm
<u>Leaf:</u>			
Number	4	2-3	2-3
Size	12-15cm x 3mm	15-19cm x 5mm	13-18cm x 2mm
Ligule	.5mm	1mm	.3mm
Spike:	9-11cm x 4mm	9-10cm x 12mm	4-5.5cm x 6-8mm
<u>Spikelet:</u>			
Number	2	2-3	1-2
Size	15-18 x 4mm	16-20 x 6mm	8-10 x 4mm
Floret	3-4	4-5	1-2
Glumes	7:11mm	6-7:11-13mm	7:8-9mm
Lemma	10-12mm	13-15mm	8-9mm
Awk	3-5mm	3-6mm	2-4mm

Fig. 5. *Eragrostis trichodes* ( x 4 )

## ERAGROSTIS TRICHODES

	<u>Exp. Gardens</u>	<u>Spikelet</u>	<u>Flowers</u>	<u>Glumes</u>	<u>Lemna</u>
1. Tall normal	Plains	6½mm	5-6	3½-4mm	3.2mm
2. Tall suppressed	Plains	3-3½mm	2-3	2.2-2½mm	2-2½mm
3. Medium sun	Main	6-9½x2mm	6-10	3½-3¾mm	3mm
4. Half-day shade	Main	5-8½x2mm	3-9	3-mm	---
5. Clone	Fertile	9x2mm	10	2½-3mm	2½mm
6. Tall adult	Fertile	3½x1.6mm	3-4	2½-3mm	3mm
7. Small adult	Fertile	3½x1mm	2	2¼-2 3/4	2½mm
8. Mown & re-grown	Woodward	3-4x1mm	1-2	2¼-2½mm	3mm
<u>Sandhills</u>					
9. Normal	Kansas	5-7(9)x2mm	5-8(10)	2-2½mm	2½mm
10. Large	Kansas	9-10x1½mm	10-11	2½-3mm	3mm

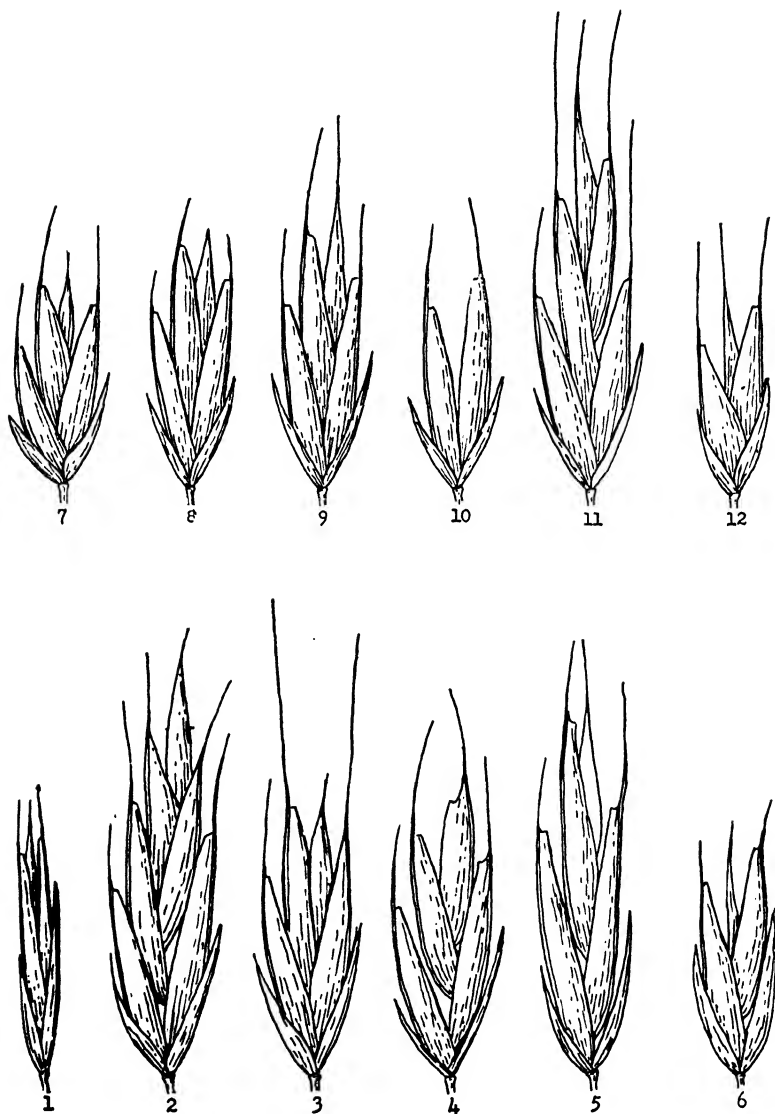


Fig. 6. *Festuca ovina* ( x 5 )

MONTANE: 1. Sun-Dry Dwarf; 2-4. Sun-Medium; 5. Half-Shade: Bush-form; 6. Half-Shade Moist: Small; 7. Half-Shade Moist: Tall; 8. Full-Shade Moist; 9. Deep-Shade Moist. SUBALPINE: 10. Sun Medium. ALPINE: 11. Sun Medium; MONTANE: 12. Sun-Dry.

## FESTUCA OVINA

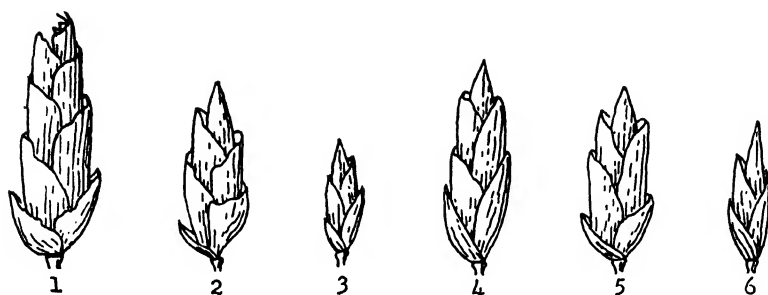
Montane Climax

<u>Criteria</u>	<u>Sun-Dry Dwarf</u>	<u>Sun-Medium 33B4</u>	<u>Sun-Medium 31 EG4</u>	<u>Sun-Medium</u>
Culm:				
Ht-diam.	18-25cm x 1mm	38cm x .7mm	40cm x 1mm	51-57cm x 1.2mm
Leaf:				
Size	7-10cm x .6mm	5-10cm x .8mm	6cm x 1mm	8cm x 2mm
Ligule	.1mm	.1mm	.1mm	.2mm
Panicle:				
Size	5cm x 4mm	9cm x 15mm	9.5cm x 8mm	10-11 x 3cm
Spikelet:				
Size	6-7 x 1mm	8-10 x 3mm	8-10 x 3mm	6-7 x 2.5mm
Floret	3	4-5	5-6	3-4
Glumes:	3:5mm	3:4mm	3.5:4.5mm	2-3.5mm
Lemma	7mm	5mm	5mm	5mm
Awns	.5-1mm	1-2.3mm	3-5mm	4mm

Montane Climax

<u>Criteria</u>	<u>Half-Shade: BushForm</u>	<u>Half-Shade Moist</u>		<u>Full-Shade Moist</u>
Culm:		<u>Small</u>	<u>Culm</u> <u>Tall</u>	
Ht-diam.	60cm x 1.5mm	24-29cm x .5mm	56-79cm x 1.5mm	10-11cm x .6mm
Leaf:				
Size	5cm x .7mm	3cm x .5mm	9cm x 1mm	3-5cm x 1mm
Ligule	.1mm	.1mm	.1mm	.1mm
Panicle:				
Size	9cm x 4mm	4-5.5cm x 2.5mm	5.5-8cm x 1cm	2.4cm x 4mm
Spikelet:				
Size	7-8mm x 2mm	6(7) x 2mm	6-7 x 3mm	6(7) x 2mm
Floret	4	2-3	3-4	2-3
Glumes	3-5mm	2-3mm	2.5-3mm	3-4mm
Lemma	6mm	4mm	5	5mm
Awns	1-2mm	1-2mm	2-2.5mm	1-3mm

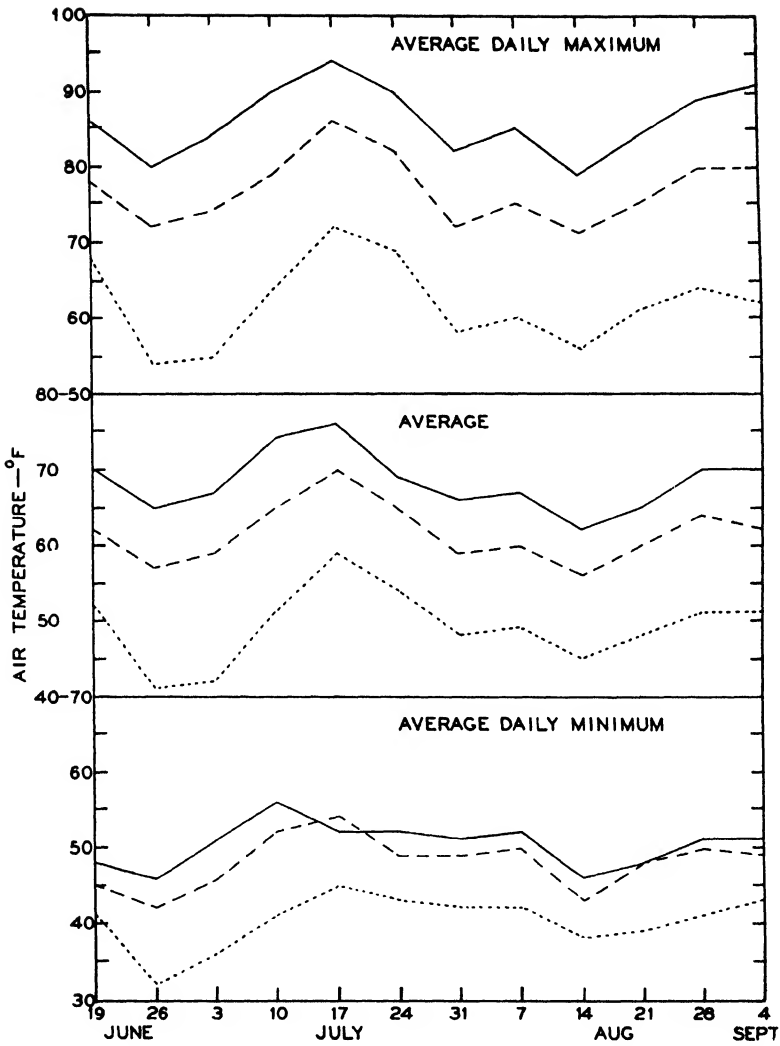
	<u>Montane Climax</u>	<u>Subalpine Climax</u>	<u>Alpine Climax</u>	<u>Montane Climax</u>
<u>Criteria</u>	<u>Deep-Shade Moist</u>	<u>Sun Medium</u>	<u>Sun Medium</u>	<u>Sun Dry</u>
Culm:				
Ht-diam.	40-70cm x 1.5mm	45-54cm x 1.5mm	23-38cm x 1mm	21-29cm x 1mm
Leaf:				
Size	8.3cm x 2mm	8-9cm x 1mm	4.5-5.5cm x 1mm	2.8-3.5mm x 1mm
Ligule	.5mm	.2mm	.2mm	.1mm
Panicle:				
Size	11cm x 1.5cm	9-12cm x 14mm	4-8cm x 1cm	4-6.5cm x 7mm
Spikelet:				
Size	4-5 x 2mm	7-8(9) x 3mm	5(6) x 2mm	5-5.5 x 2mm
Florets	1-2	4	3	4
Glumes	2.5-3mm	3-4mm	2-3mm	3-4
Lemma	5mm	5mm	4mm	4mm
Awns	1-2mm	3-4(5)mm	2-2.5mm	.5-2mm

Fig. 7. *Poa annua* ( x 5 )

1. Open ground, moist and tilled; 2. Open ground, hard, not tilled; 3. Sun gravel, hard and dry; 4. Half-day shade; 5. Herb shade, competition; 6. Oak shade, competition.

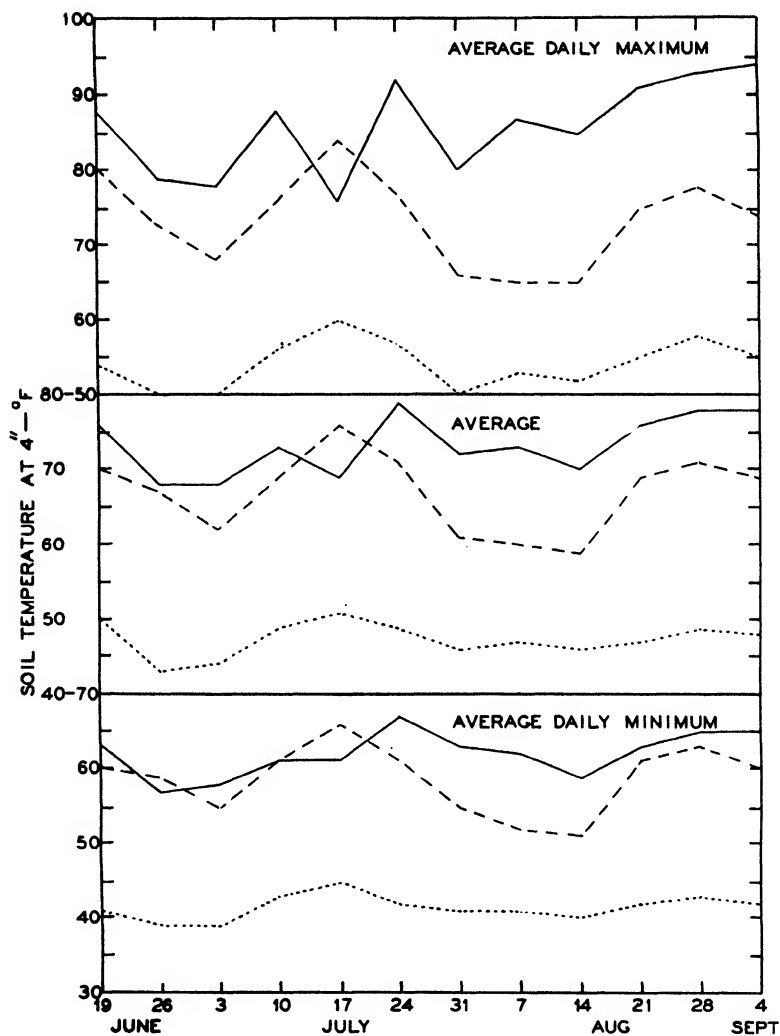
POA ANNUA: Ruderal Series

	Open ground moist & tilled	Open ground hard not tilled	Sun gravel hard & dry
Ht-diam	12-15cm x 2mm	12-15cm x 1mm	2.5-5 x .4mm
Culms	10	10	1-5
Leaf	5-7.5cm x 4-5mm	2.5-5cm x 1.5-2.5mm	8-12 x .8mm
Ligule	2.5mm	2.5mm	1mm
Panicle	4-5cm x 2-4cm	2.5-4cm x 2-4cm	1-3 x 2-3mm
Spikelet			
Florets	5-7	2-4	1-3
Size	6-7 x 2-2.5mm	3-4 x 1.5-2mm	2-2.5 x 1mm
Glumes	2.5:3mm	1.5:2mm	.8 x 1.5mm
Lemma	3mm	2.5mm	1.5-2mm
Palea	2.5mm	2mm	1-1.5mm
	Half-day shade	Herb shade Competition	Oak shade Competition
Ht-diam	25-32cm x 2mm	27-32cm x 1mm	10-15cm x .3mm
Culms	15	1	1
Leaf	6-10cm x 3-4mm	7-10 x 2.5-3mm	1-2cm x 1mm
Ligule	4mm	3mm	1mm
Panicle	7.5-9 x 5-7cm	6 x 4cm	1.5-3cm x 1-2cm
Spikelet			
Florets	3-4	3-4	1-3
Size	5-6 x 1.5-2mm	4-5 x 1.5-2mm	3.2-4 x 1-1.6mm
Glumes	2-3mm	1.3 x 2.3mm	1.8:2.2mm
Lemma	3-3.8mm	3-3.2mm	2-2.7mm
Palea	2.5-3mm	2.5-2.8mm	1.5-2mm

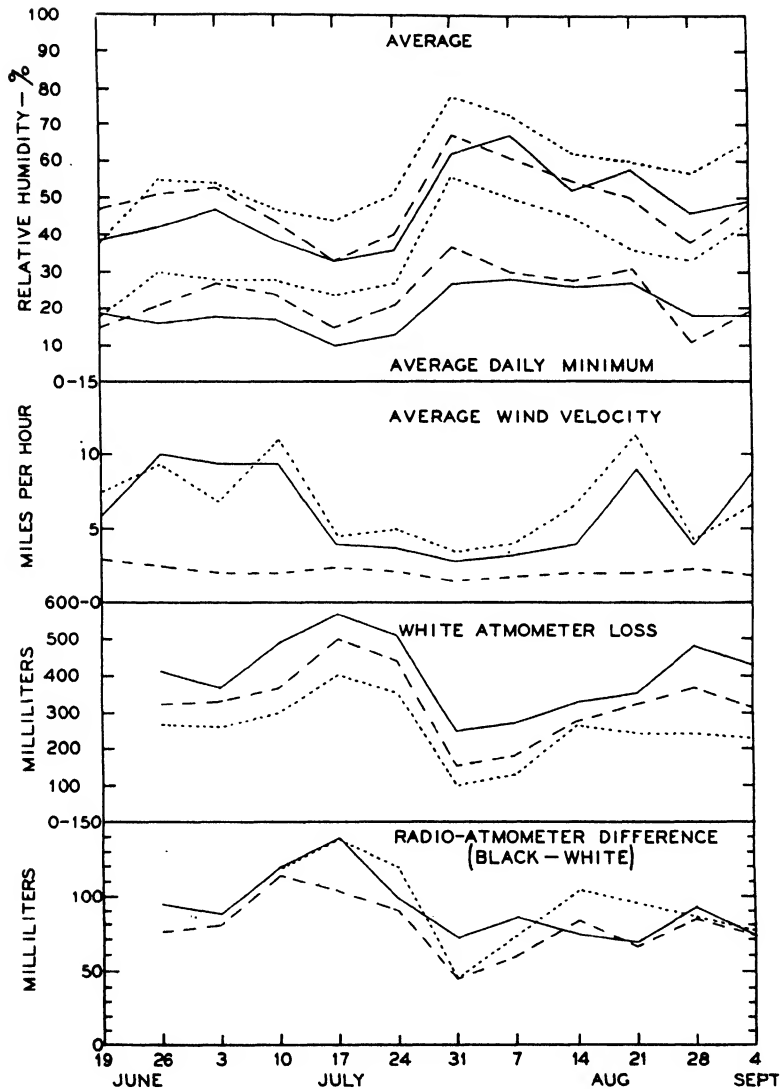


GRAPH 13. Air temperature for the summer of 1939 at the Plains (solid line), Montane sun-moist No. 1 (broken line), and Alpine sun gardens (dotted line).

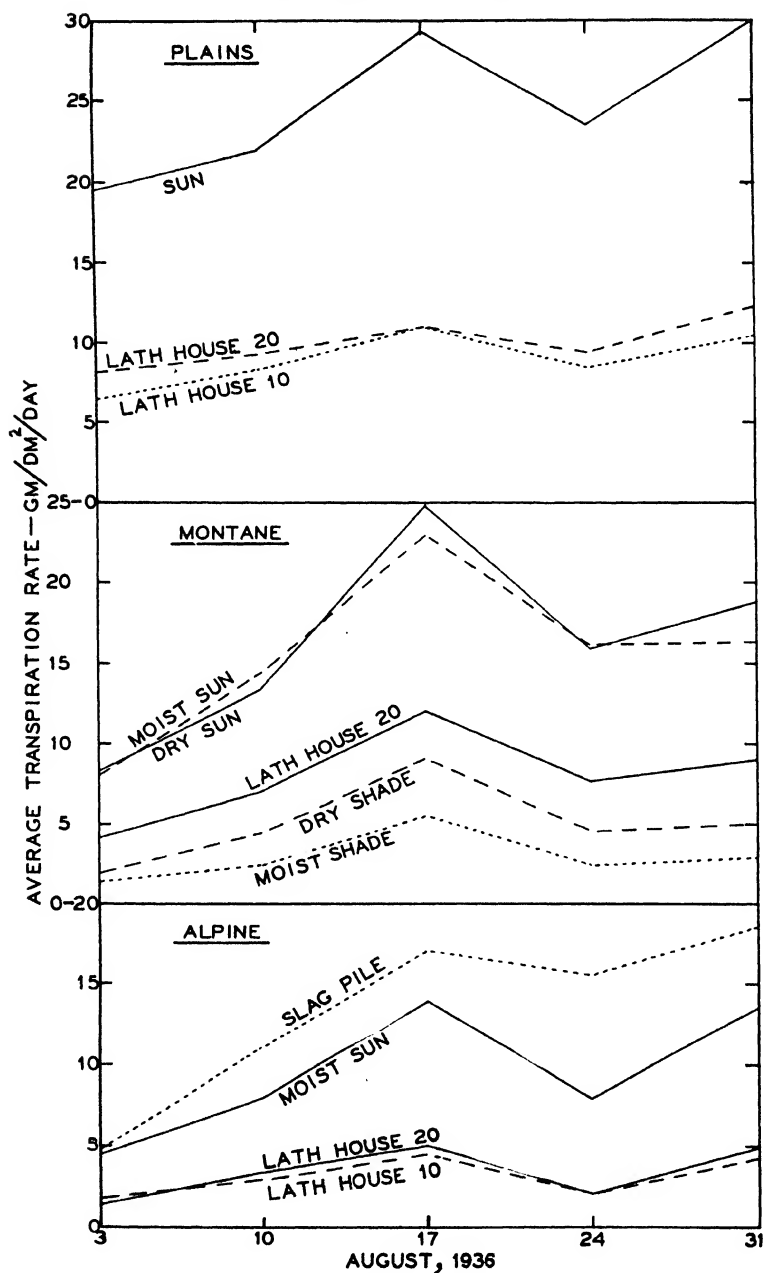




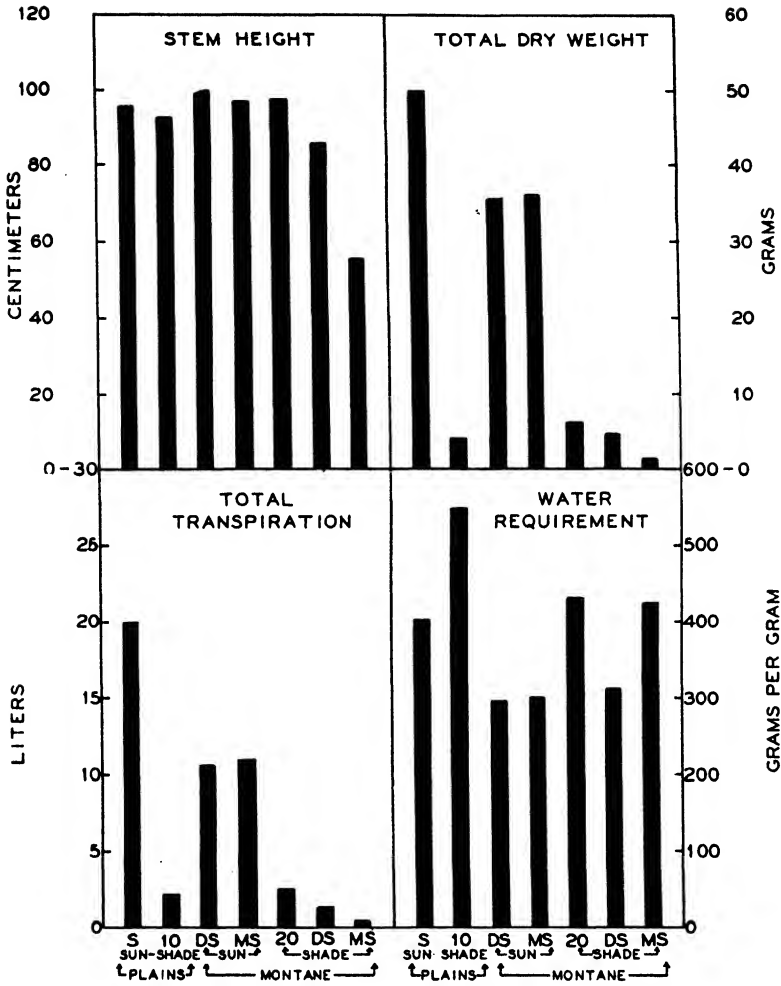
GRAPH 14. Soil temperature at a depth of 4 inches for the summer of 1939 at the Plains (solid line), Montane sun-moist No. 1 (broken line), and Alpine sun gardens (dotted line).



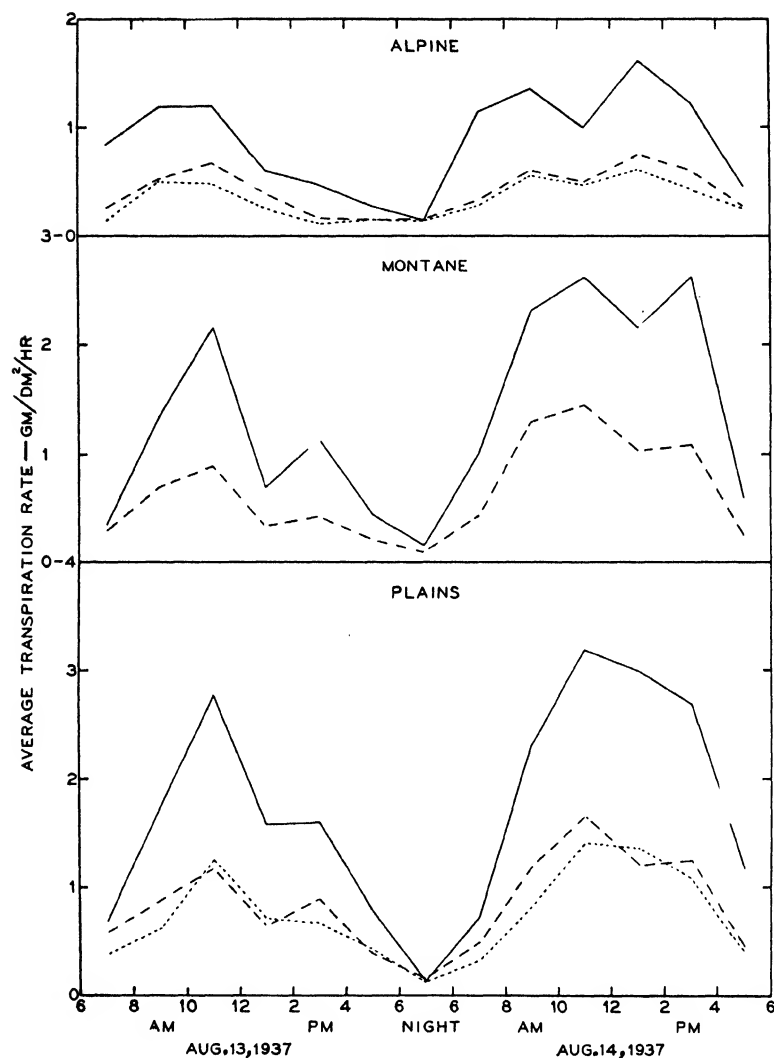
GRAPH 15. Relative humidity, wind velocity, white atmometer loss, and radio-atmometer difference for the summer of 1939 at the Plains (solid line), Montane sun-moist No. 1 (broken line), and Alpine sun gardens (dotted line).



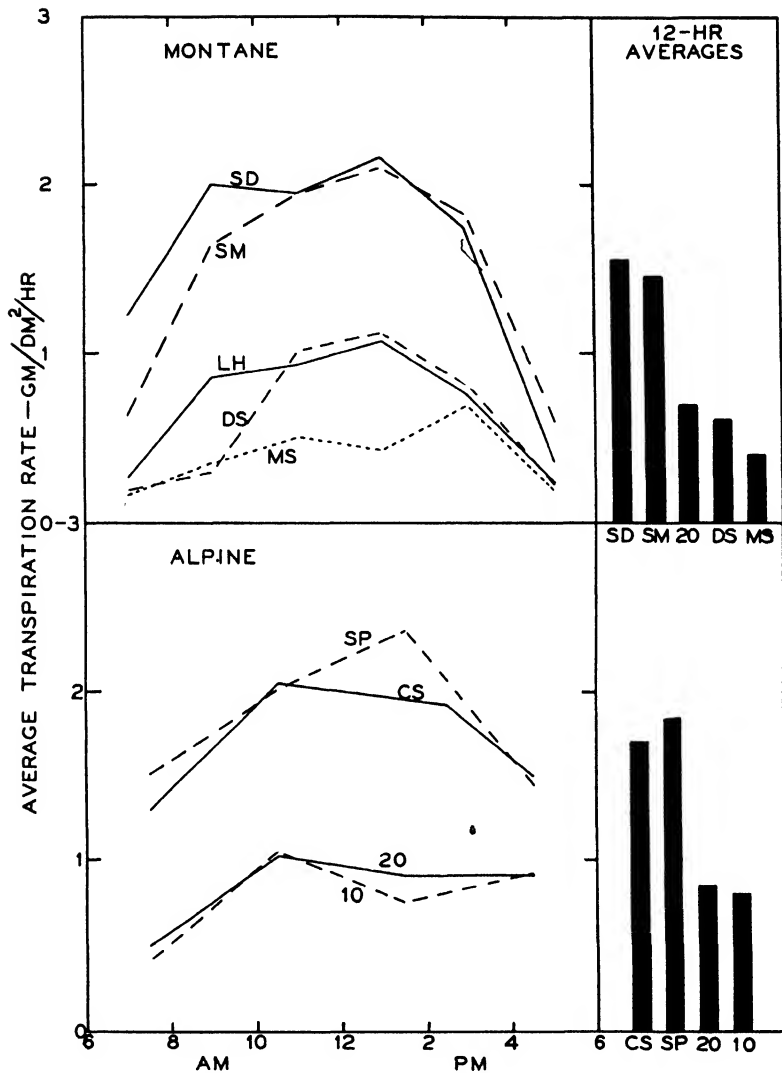
GRAPH 16. Average transpiration rate by weeks for the seasonal phytometers of *Helianthus annuus* in 1936. Values are for the week ending on dates given in abscissa.



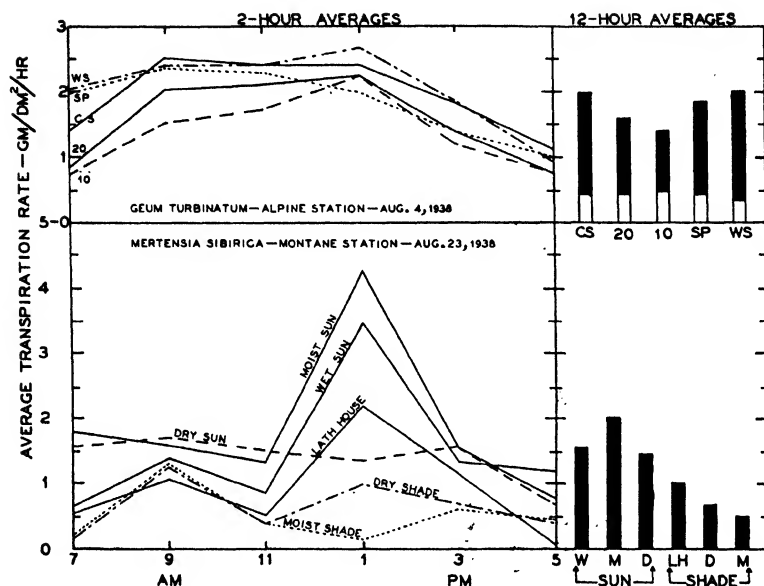
GRAPH 17. Results obtained in a seasonal series of sealed phytometers of *Helianthus annuus* in the summer of 1937. For the Plains Garden, S stands for sun and 10 for the lath-house 10%. At the Montane Garden, DS stands for dry-sun and dry-shade while MS stands for moist-sun and moist-shade as indicated in the graph. Montane shade 20 represents lath-house 20%.



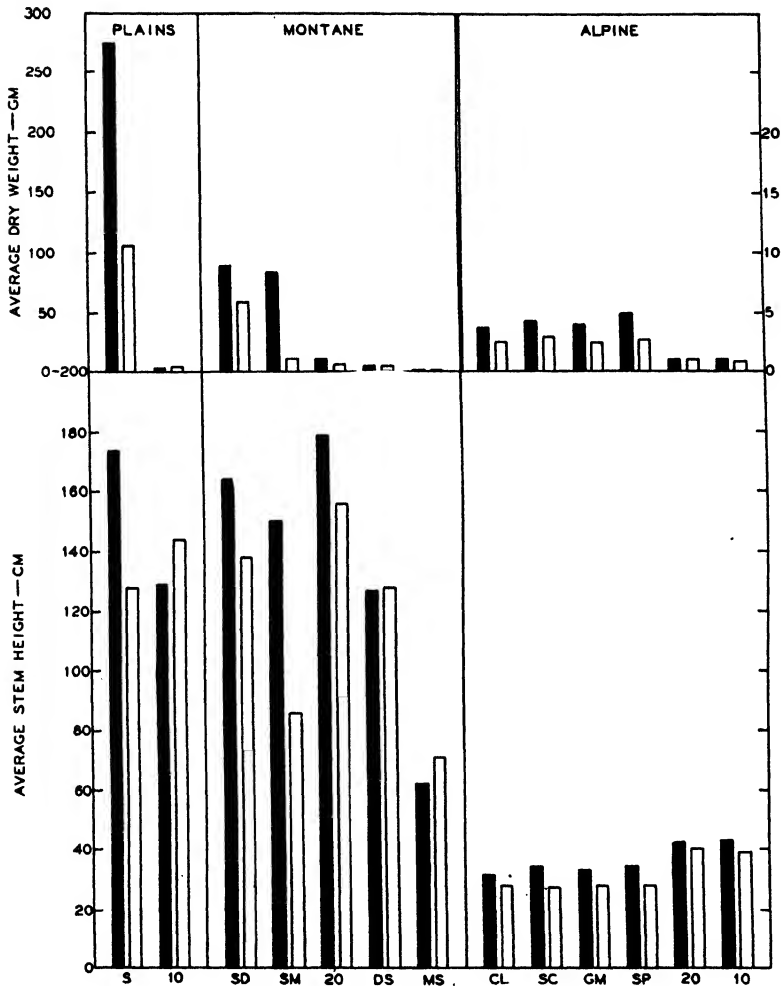
GRAPH 18. Average transpiration rates from the short-period series of sealed phytometers of *Helianthus annuus* on August 13-14, 1937. Results obtained in the sun, lath-house 20%, and lath-house 10% are shown by the solid, broken and dotted lines respectively, at all three stations.



GRAPH 19. Average transpiration rates from the short-period series with sealed phytometers of *Helianthus annuus* on August 9, 1937 at the Montane Station, and on August 26, 1936 at the Alpine Station. SD represents dry-sun, SM moist-sun, DS dry-shade, MS moist shade, CS climax sun, SP slag pile, 20 (or LH) lath-house 20%, and 10 lath-house 10%.



GRAPH 20. Average transpiration rates from a short-period series of *Geum turbinatum* at the Alpine Station on August 4, 1938. CS stands for climax sun, WS for wet-sun, SP for slag pile, 20 and 10 for lath-houses 20% and 10% respectively. For the 12-hour averages, the total column length represents the daytime average while the clear portion shows the night-time average. Results from a short-period series with sealed phytometers of *Mertensia sibirica* at the Montane Station on August 23, 1938, are also shown.



GRAPH 21. Average stem heights and dry weights (total) of free phytometers of *Helianthus annuus* (Russian Mammoth) in 1937. The solid columns represent the plants grown in imported loam while the clear columns indicate those grown in native soils. S stands for sun, SM for sun-moist, SD for sun-dry, DS for dry-shade, MS for moist-shade, CL for climax, SC for subclimax, SP for slag pile, GM for gopher mound, 20 for lath-house 20%, and 10 for lath-house 10%. The scale for the dry weights of the plants at the Alpine Station is 10 times that for the other two stations and is shown at the right side of the graph.



## ADAPTATION AND ORIGIN IN THE PLANT WORLD

Table 14. Field capacities and wilting coefficients of soils used in the soil pits at the plains, montane and alpine stations in 1937. Wilting coefficients were obtained by growing sunflowers in #3 packer's cans containing the various soils.

Station	Soil Source	Field capacity	Wilting coefficient
Plains	Sun garden	15%	5.0%
	Imported soil	19	7.1
Montane	Moist sun garden	10	3.5
	Dry sun garden	10	3.3
	Lath house 20%	10	3.0
	Dry shade garden	18	6.6
	Moist shade garden	17	6.2
	Climax	20	7.0
Alpine	Subclimax	18	6.5
	Gopher mound	16	5.1
	Slag pile	23	6.0
	Lath house 20%	15	4.9
	Lath house 10%	15	4.8

Table 15. Values of soil moisture content obtained from samples taken from the soil pits in which free phytometers of *Helianthus annuus* were grown in 1937.

Station	Habitat	Soil	Depth	Date							
				7/12	7/19	7/26	8/2	8/9	8/16	8/23	8/30
Plains	Sun	Imp.	4"	10.2	9.1	14.8	14.0	10.9	16.0	9.1	15.7
			12"	10.6	9.1	15.3	13.3	9.4	14.1	12.0	15.1
		Nat.	4	8.3	6.8	12.4	10.8	11.1	11.5	7.4	15.2
	L.R. 10%		12	8.0	10.2	12.8	14.7	11.6	14.1	10.9	15.5
		Imp.	4	13.5	11.6	10.9	13.3	12.6	17.6	14.7	19.7
			12	17.2	15.5	17.6	15.7	17.2	18.5	16.3	21.1
Montane	Dry sun	Nat.	4	12.5	12.6	12.0	12.6	14.9	13.9	13.3	17.5
			12	14.0	13.4	13.4	14.8	15.0	15.5	12.9	17.6
		Imp.	4	17.5	13.6	12.0	7.7	7.6	15.8	11.0	14.3
	Moist sun		12	19.5	17.6	13.0	7.4	7.3	14.5	8.4	13.9
		Nat.	4	9.7	8.4	7.1	4.3	5.7	10.0	4.0	11.6
			12	5.3	4.1	5.7	3.5	5.5	6.3	3.1	8.1
	L.R. 20%	Imp.	4	17.3	16.8	18.0	14.7	12.5	16.8	9.6	18.5
			12	17.5	18.2	20.3	18.6	14.1	16.9	11.4	17.0
		Nat.	4	11.4	10.8	10.1	8.5	8.4	8.3	6.9	10.7
	Dry shade		12	12.2	11.6	11.4	8.6	11.4	9.1	9.3	13.4
		Imp.	4	19.0	17.5	16.9	16.5	17.7	14.8	16.4	20.5
			12	17.2	17.7	17.0	16.4	17.5	15.2	14.7	18.5
	Moist shade	Nat.	4	10.6	8.9	8.9	6.1	6.5	6.6	8.2	11.6
			12	10.1	12.3	9.8	8.8	7.2	6.6	7.5	8.3
		Imp.	4	15.6	19.3	16.9	17.6	13.8	14.2	13.6	17.2
			12	17.3	17.4	17.1	17.4	15.5	15.1	13.7	18.3
		Nat.	4	17.8	28.1	19.5	19.6	22.4	16.6	14.2	26.0
			12	25.8	22.5	26.4	20.5	14.8	25.3	18.4	19.2
		Imp.	4	17.5	15.0	17.5	14.7	14.2	15.6	15.8	11.5
			12	22.4	22.6	20.3	21.7	19.1	20.4	24.0	13.9
		Nat.	4	8.4	14.2	8.9	9.5	9.5	7.1	11.6	13.5
			12	9.3	6.9	19.2	8.3	11.6	7.1	8.4	13.3
	Climax	Imp.	4	14.2	12.6	14.1	14.5	12.1	8.0	12.2	17.7
			12	14.1	13.1	13.9	16.3	12.8	11.5	12.0	21.0
		Nat.	4	14.0	18.9	17.8	21.2	16.7	19.2	17.8	25.6
	Subclimax		12	14.0	11.5	14.6	17.0	11.1	18.5	12.1	25.5
		Imp.	4	13.6	13.6	13.3	14.4	18.5	11.9	13.3	19.4
			12	15.0	14.2	16.3	18.5	16.4	16.2	13.1	18.8
	Gopher mound	Nat.	4	11.0	18.4	10.7	13.2	11.7	10.4	10.7	17.4
			12	10.1	11.8	9.8	13.2	11.1	11.8	9.6	16.5
		Imp.	4	14.5	15.7	15.3	15.1	15.2	16.6	17.7	24.9
			12	15.3	15.0	16.3	17.4	16.9	17.4	19.0	22.1
		Nat.	4	11.1	11.9	8.9	10.9	9.3	11.8	14.8	20.8
			12	11.1	12.0	11.9	16.1	12.3	15.4	11.2	17.0
	Slag pile	Imp.	4	13.9	14.4	13.2	14.8	12.9	16.4	16.1	19.1
			12	16.6	16.7	14.9	18.1	15.2	17.8	16.7	21.4
		Nat.	4	18.2	20.8	12.7	18.4	19.6	17.7	17.4	17.9
	L.R. 20%		12	24.3	32.9	30.9	26.0	22.3	22.7	21.0	28.9
		Imp.	4	13.2	13.9	14.3	14.9	14.1	13.2	19.4	20.7
			12	14.9	14.5	15.6	16.3	14.9	15.2	16.8	20.7
	L.R. 10%	Nat.	4	13.8	12.5	14.7	15.2	13.4	13.8	17.0	20.6
			12	11.9	12.9	15.6	14.8	14.0	14.8	16.0	17.1
		Imp.	4	14.8	14.3	13.4	18.3	15.5	17.7	12.1	23.0
			12	14.4	14.9	15.5	16.2	15.7	16.1	11.8	20.6
		Nat.	4	13.6	12.4	13.5	13.8	11.7	13.6	16.5	17.1
			12	15.8	16.2	14.0	13.5	15.2	16.4	16.7	18.4

Table 16. General information concerning the sealed phytometers employed in 1938.

Species	Station	Source	Can size	Cut back?	New leaves formed?	Planting date
<i>Caltha leptosepala</i>	Alpine	Alpine sun native	#2 $\frac{1}{2}$	No	Yes	7/1/38
<i>Geum turbinatum</i>	"	Gopher mounds	#2 $\frac{1}{2}$	No	Yes	7/1
<i>Fragaria vesca</i>	Montane	Montane sun	#2 $\frac{1}{2}$	Yes	Yes	7/8
" <i>virginiana</i>	"	" shade	#2 $\frac{1}{2}$	"	"	7/8
<i>Mertensia sibirica</i>	"	" "	5" x 8"	No	"	6/27
<i>Rubus strigosus</i>	"	" sun	5" x 5"	Yes	No	7/30
<i>Smilicina stellata</i>	"	" "	5" x 5"	No	No	6/24

Table 17. General information concerning the sealed phytometers employed in 1939.

Species	Habitat	Source	Can size	Cut back?	New leaves formed?	Planting date
Plains sun species						
<i>Helianthus annuus</i> (S-490)	Plains sun	Seed	8" x 10"			6/9/39
	Montane sun	"	8 x 10			6/9
	Montane LH	"	8 x 10			6/9
<i>Helianthus annuus</i> (Russian Mammoth)	Plains sun	Seed	8 x 10			6/9
	Montane sun	"	8 x 10			6/9
	Montane LH	"	8 x 10			6/9
<i>Mertensia lanceolata</i>	Plains sun	Native sun	#3	Yes	Yes	6/24
<i>Senecio oblancoelatus</i>	Plains sun	" "	#3	"	"	6/24
<i>Tradescantia virginiana</i>	Plains sun	" "	5" x 5"	"	"	7/22
	Plains LH	" "	5 x 5	"	"	7/22
Montane sun species						
<i>Erigeron macranthus</i>	Montane sun	Native sun	#3	Some	Few	6/21
	Montane LH	" "	#3	"	"	6/21
<i>Fragaria vesca</i>	Montane sun	Native sun	#3	Yes	Yes	6/13
	Montane LH	" "	#3	"	"	6/13
<i>Potentilla gracilis</i>	Montane sun	Native sun	#3	Yes	Yes	6/22
" <i>hippiana</i>	Montane sun	" "	#3	"	"	6/22
	Montane LH	Montane LH (Vol.)	#3	"	"	6/22
<i>Rubus strigosus</i>	Montane sun	Native sun	6" x 9"	Yes	Few	6/23
	Montane LH	Montane LH (Vol.)	6" x 9"	"	"	6/23
<i>Senecio fendleri</i>	Montane sun	Native sun	#3	Some	No	6/22
<i>Smilicina stellata</i>	Montane sun	" "	5" x 5"	No	No	6/13
	Montane LH	" shade	5 x 5	No	No	6/13
<i>Solidago missouriensis</i>	Plains sun	Native sun	#3	Yes	Yes	6/21
	Montane sun	" "	#3	"	"	6/21
	Alpine sun	Alpine sun (1937)	#3	No	Some	6/28
Montane shade species						
<i>Erigeron glabellus</i>	Montane sun	Native shade	#3	Yes	Yes	6/21
	Montane LH	" "	#3	"	"	6/21
<i>Fragaria virginiana</i>	Montane sun	" "	#3	"	"	6/13
	Montane LH	" "	#3	"	"	6/13
<i>Feracolum lanatum</i> (First series)	Plains sun	" "	8" x 10"	No	No	1938
	Plains LH	" "	8 x 10	No	No	1938
	Montane sun	" "	8 x 10	No	No	1938
	Montane LH	" "	8 x 10	No	No	1938
	Alpine sun	" "	8 x 10	No	No	1938
	Alpine LH	" "	8 x 10	No	No	1938

Table 19 (Cont.). General information concerning the sealed phytometers employed in 1939.

Species	Habitat	Source	Can size	Cut back?	New leaves formed?	Planting date
Montane shade species(Cont.)						
<i>Heracleum lanatum</i> (Second series)	Montane sun Montane LH	Native shade " "	8"x 10" 8 x 10	Yes "	Yes "	6/10 6/10
<i>Mertensia sibirica</i> (First series)	Plains sun	" "	5 $\frac{1}{2}$ " x 8"	No	Few	1938
	Plains LH	" "	5 $\frac{1}{2}$ x 8	No	Few	1938
	Montane sun	" "	5 $\frac{1}{2}$ x 8	"	"	1938
	Montane LH	" "	5 $\frac{1}{2}$ x 8	"	"	1938
	Alpine sun	" "	5 $\frac{1}{2}$ x 8	"	"	1938
	Alpine LH	" "	5 $\frac{1}{2}$ x 8	"	"	1938
<i>Mertensia sibirica</i> (Second series)	Montane sun	" "	5 $\frac{1}{2}$ x 8	Yes	Yes	1938
	Montane LH	" "	5 $\frac{1}{2}$ x 8	No	"	1938
	Alpine sun	Native alpine sun	5 $\frac{1}{2}$ x 8	No	"	6/28
	Alpine LH	Alpine LH(1932)	5 $\frac{1}{2}$ x 8	No	"	6/28
<i>Mertensia viridus</i>	Montane LH	Native shade	#3	Yes	Yes	6/22
<i>Senecio cernuus</i>	Montane sun	Montane sun(1932)	#3	No	No	6/22
	Montane LH	Native shade	#3	No	Yes	6/22
<i>Solidago humilis</i>	Plains sun	Native shade	#3	Yes	Yes	6/21
	Montane sun	" "	#3	"	"	6/21
	Montane LH	" "	#3	"	"	6/21
	Alpine sun	Alpine sun(1932)	#3	No	Some	6/28
Subalpine sun species						
<i>Senecio bigelovi</i>	Montane sun	Montane sun(1938)	6"x 8"	No	Few	7/9
	Alpine sun	Timberline	#3	No	Yes	6/28
Alpine sun species						
<i>Geum turbinatum</i>	Plains sun	Plains sun(1935)	#3	No	Yes	6/24
	Montane sun	Montane sun(1932)	#3	No	"	6/21
	Montane LH	Montane LH (1932)	#3	"	"	6/21
	Alpine sun	Native sun	#3	"	"	6/28
	Alpine LH	Alpine LH (1932)	#3	"	"	6/28
	Plains LH	Native sun	#2 $\frac{1}{2}$	"	"	1938
	Montane LH	" "	#2 $\frac{1}{2}$	"	"	1938
	Alpine LH	" "	#2 $\frac{1}{2}$	"	"	1938
<i>Mertensia alpina</i>	Alpine sun	" "	#2 $\frac{1}{2}$	No	Yes	1938
	Alpine LH	" "	#2 $\frac{1}{2}$	"	"	1938
<i>Potentilla nivea</i>	Alpine sun	" "	#3	No	Yes	6/28
	Alpine LH	" "	#3	"	"	6/28
" <i>rubricaulis</i>	Plains sun	Plains sun(1935)	#3	"	"	6/24
	Alpine sun	Native sun	#3	"	"	6/28
	Alpine LH	Alpine LH(1932)	#3	"	"	6/28
<i>Primula angustifolia</i>	Montane LH	Montane LH(1932)	#3	No	No	6/22
	Alpine sun	Native sun	#3	"	"	6/28

Table 18. General information concerning the sealed phytometers employed in 1940.

Species	Habitat	Source	Can size	Cut bank?	New leaves formed?	Planting date
Montane sun species						
Erigeron macranthus	Montane sun	Native sun	#3	No	Yes	6/19/40
	Montane LH	Montane shade(1938)	#3	"	"	6/19
Montane shade species						
Mertensia sibirica	Montane sun	Native shade	5 1/2" x 8"	Yes	Yes	6/13
	Montane LH	" "	5 1/2" x 8"	"	"	6/13
	Alpine sun	" "	5 1/2" x 8"	"	"	6/13
	Alpine LH	" "	5 1/2" x 8"	"	"	6/13
	Alpine sun	" alpine sun	6" x 9"	No	"	6/25
	Alpine LH	" shade(1932)	6" x 9"	"	"	6/25
Senecio cernuus	Montane sun	Montane sun(1932)	#3	No	No	6/19
	Montane LH	Native shade	#3	"	"	6/19
Subalpine sun species						
Senecio bigelovi	Montane sun	Montane sun(1938)	6" x 8"	No	No	6/19
	Alpine sun	Timberline	#3	"	Yes	6/25
Alpine sun species						
Potentilla nivea	Alpine sun	Native sun	#3	No	Yes	6/25
	Alpine LH	" "	#3	Yes	"	6/25
Potentilla rubricaulis	Alpine sun	" "	#3	No	"	6/25
	Alpine LH	Alpine LH(1938)	#3	"	"	6/25
Senecio aureus croceus	Montane sun	Native sun	#3	Yes	Yes	6/25
	Alpine sun	" "	#3	"	"	6/25
Senecio taraxacoides	Alpine sun	" "	#3	No	"	6/25
	Alpine LH	Alpine LH(1938)	#3	"	"	6/25

Table 19. Averages of certain meteorological factors at the three climatic stations for the years 1936 to 1940, inclusive.

Year	Station	Weeks	Air temperature			Rel. Hum.		Average Wind Vel.	Season Rainfall	Av. corr. white atmometer loss
			Av. Max.	Av. Min.	Op	Av.	Av. Min.			
			°F	°F	°F	%	%	mph.	inches	ml/week
1936	Plains	14	86	68	54	60	31	3.06	8.28	
	Montane	14	74	61	52	63	40	1.75	10.32	
	Alpine	14	61	48	40	62	41	4.78	13.19	
1937	Plains	11	89	70	53	55	27	3.02	4.26	348
	Montane	11	77	65	56	59	33	1.43	4.51	320(3)
	Alpine	11	60	48	39	60	37	3.98	6.83	203
1938	Plains	10	85	68	52	54	25	3.69	2.63	565
	Montane	10	75	61	45	57	31	1.67	6.08	250(6)
	Alpine	10	60	48	39	64	38	4.64	7.63	192
1939	Plains	12	86	68	51	48	20	6.18	2.17	406
	Montane	12	77	62	48	48	23	2.11	2.51	325(11)
	Alpine	12	62	49	40	57	35	6.77	5.62	258
1940	Plains	11	86	68	51	58	27	2.58	3.15	375
	Montane	11	78	60	49	60	33	1.30	6.08	281(10)
	Alpine	11	57	46	37	62	40	4.95	6.97	215

Numbers in parentheses after atmometer losses indicate number of weeks for which these values are averages. All values for a given year are for the same number of weeks.

Table 20. Values of soil moisture content in percentage of the dry weight of the soil from various habitats in the adaptation gardens in 1938.

Station	Habitat	Depth	Date									
			7/18	7/21	7/25	7/28	8/1	8/8	8/15	8/22	8/29	
Plains	Wet alpine	8"	11.5	11.2	12.3	10.6	12.6	11.6	11.8	12.1	12.1	
		16	14.6	11.6	12.9	12.2	16.2	13.9	14.8	16.5	15.9	
	Dry alpine	8	10.0	11.5	9.1	9.0	8.1	8.8	9.6	9.4	10.8	
		16	8.9	9.7	9.0	9.3	8.0	8.9	8.9	9.5	9.5	
	Lath house	8	18.7	14.4	15.3	13.9	11.8	14.2	17.5	17.1	15.5	
		16	13.9	18.6	15.9	17.5	16.6	17.9	15.8	17.8	18.0	
Montane	Dry sun	8	5.7	14.0	6.4	10.0	2.8	1.9	12.9	11.7	24.5	
		16	5.4	5.8	5.3	8.1	2.2	4.7	6.7	11.4	35.5	
	Moist sun	8	10.1	12.5	2.5	13.6	6.0	8.9	10.3	14.4	13.1	
		16	13.6	5.9	1.6	7.3	3.6	10.2	13.2	12.4	11.6	
	Wet sun	8	13.8	5.3	10.0	9.4	6.4	12.2	10.8	13.3	12.7	
		16	7.4	11.6	7.4	8.1	6.7	7.2	8.2	10.8	10.1	
	Dry shade	8	10.3	13.8	5.5	8.9	5.1	10.7	17.4	10.1	9.9	
		16	10.0	13.8	8.1	8.9	25.8	13.7	17.3	11.3	9.9	
	Moist shade	8	9.8	9.9	44.8	21.1	5.0	14.9	28.4	10.4	15.0	
		16	8.8	7.5	12.8	14.3	13.2	11.3	10.8	14.6	17.9	
	Lath house	8	----	25.3	6.2	7.3	6.2	8.3	11.9	10.4	15.4	
		16	----	20.6	15.7	19.8	6.7	15.0	18.2	20.2	9.8	
Alpine	Climax	4	23.8	29.0	19.1	16.2	21.6	21.6	26.2	27.6	14.0	
		12	18.8	25.3	14.7	19.0	11.9	14.9	18.5	18.6	12.8	
	Subclimax	4	5.7	6.6	14.8	21.2	13.1	12.9	10.5	11.4	11.6	
		12	13.4	15.4	12.7	15.4	10.3	11.8	13.6	10.1	5.8	
	Gopher mound	4	16.8	13.5	12.7	13.8	13.3	11.3	11.9	9.0	12.3	
		12	16.6	15.7	14.3	16.1	14.1	10.0	10.9	12.8	11.4	
	Slag pile	4	26.2	28.6	24.2	27.4	23.5	18.0	24.7	14.7	17.7	
		12	29.4	38.3	49.2	37.8	30.1	20.6	37.2	16.9	19.9	
	Lath house 20%	4	18.9	18.5	18.6	15.7	11.8	13.9	14.2	13.0	14.0	
		12	23.4	12.7	18.0	15.2	13.5	12.2	13.0	12.0	17.2	
	Lath house 10%	4	17.4	14.6	15.1	21.6	16.1	18.4	16.7	20.8	15.4	
		12	13.2	16.8	23.1	26.9	25.8	16.2	21.8	21.2	23.2	
	Climax soil pit	4	19.7	24.4	19.4	18.3	31.3	15.5	15.5	13.3	17.4	
		12	17.7	28.8	18.1	17.6	19.3	14.5	15.6	14.6	15.4	
	Gopher mound soil pit	4	12.6	17.8	13.3	16.4	13.5	12.2	13.9	7.1	12.4	
		12	12.7	15.0	14.6	15.7	14.2	11.0	12.8	7.9	12.6	
	Adobe soil pit	4	28.0	26.0	24.0	24.0	22.6	19.7	23.4	20.0	24.6	
		12	27.6	27.3	24.2	23.6	25.4	20.6	22.6	20.5	22.2	
	Sand soil pit	4	4.5	3.7	4.0	4.4	2.9	2.8	3.6	2.6	4.2	
		12	4.5	4.1	3.4	3.9	4.0	2.5	3.4	2.6	4.1	

Depths of samples are in inches.

## TABLES

287

Table 21. Transpiration in grams per plant and in grams per square decimeter of leaf surface per day from the sealed phytometer series of *Helianthus annuus* in 1936.

Week ending		Aug. 3		Aug. 10		Aug. 17		Aug. 24		Aug. 31	
Station	Habitat	Loss	Rate	Loss	Rate	Loss	Rate	Loss	Rate	Loss	Rate
Plains	Sun	723	19.6	1200	22.0	1800	29.4	1535	23.6	1952	30.0
	L.H. 20%	322	8.2	584	9.3	778	11.0	742	9.5	995	12.2
	L.H. 10%	228	6.5	461	8.3	696	10.9	583	8.6	733	10.4
Montane	Dry sun	297	8.3	592	13.4	1247	24.9	948	15.9	1168	18.8
	Moist sun	305	8.0	674	14.4	1301	25.1	946	16.2	1090	16.3
	L.H. 20%	149	4.2	310	7.0	664	12.2	488	7.7	638	8.9
	Dry shade	71	1.8	203	4.5	497	9.1	295	4.7	336	5.0
	Moist "	51	1.4	94	2.3	252	5.5	118	2.4	144	2.6
Alpine	Sublimex	74	4.6	135	7.9	230	14.0	122	7.9	208	13.6
	L.H. 20%	22	1.5	62	3.4	86	5.1	38	2.2	88	4.9
	L.H. 10%	31	1.9	54	3.1	85	4.6	42	2.2	92	4.4
	Slag pile	70	4.8	171	11.0	245	17.1	211	15.6	238	18.6

Loss is in grams per plant per day and Rate is in grams per square decimeter per day. L.H. means lath house.

Table 22. Transpiration in grams per plant and in grams per square decimeter of leaf surface per day from the sealed phytometer series of *Helianthus annuus* in 1937.

Week ending		July 5		July 12		July 19		July 26	
Station	Habitat	Loss	Rate	Loss	Rate	Loss	Rate	Loss	Rate
Plains	Sun	1148	32.9	2455	24.6	5175	21.7	11009	21.9
	L.H. 10%	363	15.7	591	15.1	397	6.0	907	10.3
Montane	Dry sun	726	25.8	1558	19.3	2458	14.7	5827	16.5
	Moist sun	739	26.4	1647	19.7	2769	15.4	5879	14.2
	L.H. 20%	356	15.7	556	12.6	584	7.9	1240	9.8
	Dry shade	241	11.5	303	7.8	320	5.4	605	6.1
	Moist "	217	11.6	117	4.0	99	3.1	140	3.6

Loss is in grams per plant per day and Rate is in grams per square decimeter per day. L.H. means lath house.

Table 23. Summary of data obtained from sealed phytometers of *Helianthus annuus* in 1936 and 1937. Dates of final measurements were Aug. 31, 1936 and Aug. 30, 1937.

1936												
Station	Habitat	Stem height	Stem diam.	Leaf area	No. of leaves	Fresh weight	Dry weight	Total water loss	W.R.	No. of plants	% water	
Plains	Sun	85	0.84	9.0	17	88.0	15.13	7210	465	11	82.8	
	L.H. 20%	112	0.79	11.5	15	59.6	7.18	3373	462	11	86.0	
	L.H. 10%	92	0.72	10.3	14	40.0	4.28	2703	649	9	89.3	
Montane	Dry sun	82	0.89	9.1	19	56.8	9.76	4335	476	11	86.4	
	Moist sun	85	0.92	9.9	19	64.4	12.29	4315	357	12	80.9	
	L.H. 20%	104	0.82	10.9	17	48.6	5.88	2280	391	11	87.9	
	Dry shade	80	0.85	10.8	16	50.8	4.98	1340	293	12	90.5	
	Moist "	63	0.70	7.4	12	28.0	2.53	677	256	11	89.3	
Alpine	Sublimex	35	0.61	2.1	9	23.3	3.18	769	---	11	86.4	
	L.H. 20%	41	0.48	2.7	8	15.5	1.60	874	---	11	89.7	
	L.H. 10%	40	0.54	3.1	10	15.6	1.72	304	---	11	89.0	
	Slag pile	31	0.53	1.6	9	15.6	2.91	954	---	11	81.3	
1937												
Plains	Sun	96	1.77	72.0	28	397	49.5	19909	403	9	87.5	
	L.H. 10%	93	0.80	12.7	14	53.0	4.15	2266	549	12	92.6	
Montane	Dry sun	100	1.81	51.9	28	320	35.8	10586	296	12	88.1	
	Moist sun	97	1.84	58.3	28	350	36.4	10947	301	12	89.0	
	L.H. 20%	98	0.99	18.1	18	85.0	6.30	2719	432	12	92.8	
	Dry shade	96	0.80	13.9	16	65.5	4.71	1468	312	12	92.8	
	Moist "	56	0.60	5.8	11	18.4	1.35	573	424	12	92.5	

L.H. means lath house, and W.R. means water requirement.

Table 24. Results of short-period series with phytometers of various species in selected habitats at the montane and alpine stations.

Species Station Date	Habitat	Time period						Av. 6-6
		6-8	8-10	10-12	12-2	2-4	4-6	
<i>Caltha leptosepala</i> Alpine station Aug. 4, 1938	Climax sun	1.10	1.24	1.54	1.68	0.98	0.62	1.23
	Lath house	0.81	1.03	1.06	1.18	0.73	0.52	0.90
	Lath house	0.47	0.64	0.57	0.70	0.45	0.31	0.62
	Slag pile	0.80	1.62	1.41	1.59	0.76	0.57	1.06
	Wet sun(pool)	0.75	1.79	1.63	1.68	0.96	0.77	1.34
<i>Geum turbinatum</i> Alpine station Aug. 4, 1938	Climax sun	1.39	2.52	2.40	2.42	1.84	1.12	1.98
	Lath house	0.85	2.04	2.12	2.25	1.39	0.74	1.58
	Lath house	0.73	1.51	1.72	2.24	1.21	0.75	1.38
	Slag pile	1.98	2.36	2.30	2.00	1.41	1.00	1.86
	Wet sun(pool)	2.02	2.40	2.40	2.68	1.90	0.84	2.02
<i>Smilicina stellata</i> Montane station July 27, 1938	Wet sun	0.27	0.86	0.32	0.81	0.54	0.10	0.49
	Moist sun	1.28	0.95	0.58	0.67	0.77	0.26	0.73
	Dry sun	0.83	0.56	1.28	0.98	1.21	0.35	0.90
	Lath house	0.74	0.66	0.65	0.43	0.70	0.16	0.56
	Dry shade	0.05	0.15	0.96	0.61	0.70	0.03	0.43
<i>Mertensia sibirica</i> Montane station July 27, 1938	Moist shade	0.07	0.07	0.29	0.52	0.30	0.38	0.25
	Wet sun	0.67	1.40	0.87	3.46	1.35	1.21	1.57
	Moist sun	1.81	1.49	1.33	4.26	1.57	0.79	2.02
	Dry sun	1.59	1.73	1.52	1.36	1.57	0.68	1.47
	Lath house	0.54	1.06	0.52	2.20	1.16	0.06	1.01
<i>Rubus strigosus</i> Montane station Aug. 23, 1938	Dry shade	0.17	1.24	0.40	0.98	0.68	0.41	0.67
	Moist shade	0.22	1.31	0.41	0.13	0.61	0.44	0.52
	Wet sun	6-10		10-2		2-6		6-6
	Moist sun	0.70		0.65		0.51		0.62
	Dry sun	1.02		0.90		0.55		0.82
<i>Fragaria vesca</i> Montane station Aug. 23, 1938	Lath house	1.28		0.88		0.97		1.05
	Dry shade	0.64		0.62		0.61		0.54
	Dry shade	0.24		0.38		0.80		0.47
	Moist shade	0.18		0.60		0.75		0.51
	Wet sun	1.25		1.51		0.59		1.12
<i>Fragaria virginiana</i> Montane station Aug. 23, 1938	Moist sun	2.18		1.65		0.96		1.60
	Dry sun	2.18		1.79		2.32		2.22
	Lath house	1.28		0.79		0.50		0.87
	Dry shade	0.59		0.78		2.14		1.17
	Moist shade	0.83		0.65		1.75		1.07
<i>Fragaria virginiana</i> Montane station Aug. 23, 1938	Wet sun	1.25		1.46		0.71		1.14
	Moist sun	2.32		1.72		0.93		1.65
	Dry sun	2.76		1.63		1.97		2.12
	Lath house	1.49		0.97		0.71		1.06
	Dry shade	0.68		0.67		1.47		0.84
<i>Fragaria virginiana</i> Montane station Aug. 23, 1938	Moist shade	0.63		0.77		1.74		1.06

Values given are the transpiration rates in grams per square decimeter per hour, employing unilateral leaf areas.

Table 25. Data obtained in 1939 from short-period series with sun and shade forms.

Species	Station	Series Location	Hours of series	Av. transpiration rate		Prob.	No. plants	
				Sun	Shade		Sun	Shade
<i>Helianthus annuus</i> (RM)	Montane	NH	56	2.82	1.272	<.01	8	8
		Shade	27	0.578	0.566			
		Sun	24	1.316	1.078	<.01		
		NH	56	2.80	1.152	<.01	9	9
<i>Helianthus annuus</i> (Can.)	Montane	Shade	27	0.592	0.536	.25		
		Sun	24	1.248	0.980	<.01		
<i>Smilicina stellata</i>	Montane	NH	72	0.374	0.285	.048	9	9
		Shade	72	0.656	0.570	.4		
		Sun	81	0.748	0.532	.05		
<i>Heracleum lanatum</i> (First series)	Plains	NH	56	1.62	1.04	.017	6	5
		Shade	48	0.135	0.149	.22		
		Sun	77	0.533	0.473	.63		
	Montane	NH	56	1.59	0.54	.013	5	5
		Shade	48	0.100	0.126	.38		
		Sun	77	0.510	0.426	.47		
	Alpine	NH	56	1.39	0.72	<.01	6	6
		Shade	48	0.160	0.156	.9		
		Sun	77	0.749	0.667	.4		
<i>Heracleum lanatum</i> (Second series)	Montane	NH	50	0.98	0.52	<.01	10	10
		Shade	49	0.97	0.98			
		Sun	22	1.26	1.22	.5		
<i>Mertensia sibirica</i> (First series)	Plains	NH	56	1.20	0.73	.05	2	4
		Shade	48	0.155	0.142	.4		
		Sun	77	0.506	0.345	.035		
	Montane	NH	56	1.07	0.59	<.01	4	5
		Shade	48	0.155	0.127	.3		
		Sun	77	0.497	0.370	.06		
	Alpine	NH	56	1.17	0.83	.26	5	3
		Shade	48	0.228	0.294	.2		
		Sun	77	0.697	0.815	.55		
<i>Mertensia sibirica</i> (Second series)	Montane	NH	6	2.17	0.70	<.01	8	5
		NH	5	1.54	0.63	<.01		
		Shade	47	0.73	0.71			
	Alpine	Sun	8	3.97	2.74	<.01	7	5
		NH	6	1.01	0.99	.8		
		NH	5	1.39	1.04	.45		
		Shade	47	0.71	0.67	.65		
		Sun	8	2.32	2.47	.3		
<i>Senecio aureus croceus</i>	Montane	NH	7	5.60	2.07	<.01	9	10
		NH	24	2.06	0.79	<.01		
		Shade	40	0.558	0.579	.7		
		Sun	8	5.41	3.58	<.01		
<i>Senecio cernuus</i>	Montane	NH	7	3.46	1.95	<.01	7	10
		NH	24	1.47	0.56	<.01		
		Shade	40	0.558	0.334	<.01		
		Sun	8	3.91	2.69	.067		



Table 25 (Cont.). Data obtained in 1939 from short-period series with sun and shade forms.

Species	Station	Series Location	Hours of series	Av. transpiration rate		Prob.	No. plants	
				Sun	Shade		Sun	Shade
<i>Senecio taraxacoides</i>	Alpine	NH	7	2.52	1.01	<.01	10	7
		NH	24	1.01	0.78	.058		
		Shade	40	0.352	0.609	.01		
		Sun	8	3.67	3.72	.8		
<i>Geum turbinatum</i>	Plains	NH	7	3.18	2.36	.01	8	5
		NH	24	1.31	0.83	.01		
		Shade	40	0.398	0.417	.7		
		Sun	8	3.25	2.32	.02		
	Montane	NH	7	2.74	1.45	.01	8	8
		NH	24	1.28	0.67	.01		
		Shade	40	0.424	0.424	.13		
		Sun	8	3.13	2.03	.01		
	Alpine	NH	7	1.87	1.47	.5	8	8
		NH	24	0.84	1.02	.5		
		Shade	40	0.518	0.529	.12		
		Sun	8	2.60	3.94	.015		
<i>Rubus strigosus</i>	Montane	NH	31	1.18	0.79	.01	5	5
		Shade	45	0.368	0.472	.08		
		Sun	47	0.443	0.408	.32		
<i>Fragaria vesca</i>	Montane	NH	31	1.82	1.08	.01	5	6
		Shade	45	0.560	0.558	.19		
		Sun	47	0.569	0.549	.8		
<i>Fragaria virginiana</i>	Montane	NH	31	1.65	0.95	.01	7	8
		Shade	45	0.406	0.549	.01		
		Sun	47	0.598	0.547	.15		
<i>Erigeron glabellus</i>	Montane	NH	31	1.42	0.75	.01	10	8
		Shade	45	0.410	0.374	.43		
		Sun	47	0.538	0.473	.1		
<i>Erigeron macranthus</i>	Montane	NH	31	1.25	1.02	.07	13	9
		Shade	45	0.311	0.505	.015		
		Sun	47	0.547	0.584	.5		
<i>Solidago nana</i>	Montane	NH	6	1.80	0.90	.01	6	10
		NH	5	2.03	0.71	.01		
		Shade	47	0.56	0.45	.028		
		Sun	8	2.71	1.99	.019		
	Alpine	Sun	9	2.06	1.20	.01	10	8
		NH	6	0.77	1.47	.11		
		NH	5	0.95	1.51	.09		
		Shade	47	0.63	0.78	.12		
		Sun	8	4.31	4.16	.8		
		Sun	9	3.29	2.18	.01		
<i>Solidago humilis</i>	Montane	NH	6	2.06	0.99	.01	10	14
		NH	5	2.13	1.03	.01		
		Shade	47	0.77	0.84	.27		
		Sun	8	4.22	3.53	.20		
		Sun	9	2.82	2.36	.30		
<i>Mertensia alpina</i>	Alpine	NH	6	1.01	0.99	.8	7	5
		NH	5	1.39	1.04	.45		
		Shade	47	0.97	1.22	.44		
		Sun	8	2.87	3.45	.30		
<i>Potentilla hippiana</i>	Montane	NH	6	3.03	2.03	.013	6	5
		Shade	47	0.40	0.53	.054		
		Sun	30	1.07	1.15	.5		
<i>Potentilla nivea</i>	Alpine	NH	6	3.53	1.48	.01	10	10
		Shade	47	0.56	0.47	.01		
		Sun	30	1.77	1.25	.01		
<i>Potentilla rubricaulis</i>	Alpine	NH	6	3.56	1.15	.01	10	6
		Shade	47	0.64	0.49	.02		
		Sun	30	1.92	1.25	.01		
<i>Primula angustifolia</i>	M. shade A. sun	NH	6	2.41	1.99	.035	9	8
		Shade	47	0.50	0.58	.15		
		Sun	30	1.17	1.11	.57		
<i>Tradesantia virginiana</i>	Plains	NH	6	2.51	1.22	.012	6	6
		NH	5	2.02	0.90	.038		
		Shade	68	0.72	0.49	.2		
		Sun	9	2.42	1.51	.14		

NH stands for native habitats, meaning that for these series the sun form plants were in the sun, and the shade form plants were in the shade of the lath house, these being the habitats in which the plants were grown.

The transpiration rates are calculated in grams per square decimeter per hour, in which the leaf area for only one side of the leaves is used.

Prob. stands for the probability that the two samples in question belong to the same population. The few missing cases of probability represent those in which the two values are so close together that a test was not deemed necessary.

## TABLES

291

Table 26. Data obtained in 1940 from short-period series with sun and shade forms.

Species	Station	Series Location	Hours of series	Av. transpiration rate		Prob.	No. plants	
				Sun	Shade		Sun	Shade
<i>Mertensia sibirica</i>	Montane	NH	6	0.86	0.43	.01	10	9
		Shade	69	0.334	0.379	.3		
	Alpine	Sun	5	1.42	1.74	.13		
		NH	6	0.82	0.368	.01	10	10
		Shade	69	0.341	0.278	.01		
		Sun	5	0.97	0.79	.033		
<i>Senecio cernuus</i>	Montane	NH	6	3.58	1.10	.01	10	9
		Shade	45	0.364	0.158	.01		
		Sun	6	2.42	0.99	.01		
<i>Senecio taraxacoides</i>	Alpine	NH	6	2.63	1.65	.055	8	9
		Shade	45	0.323	0.436	.07		
		Sun	6	2.03	2.50	.12		
<i>Erigeron macranthus</i>	Montane	NH	5	1.70	0.78	.01	10	10
		Shade	26	0.33	0.29	.15		
		Sun	6	2.17	1.76	.011		
<i>Potentilla nivea</i>	Alpine	NH	5	1.83	0.80	.12	9	4
		Shade	26	0.52	0.53	.45		
		Sun	6	3.13	3.34	.74		
<i>Potentilla rubricaulis</i>	Alpine	NH	5	1.42	0.70	.034	8	4
		Shade	26	0.61	0.52	.5		
		Sun	6	3.79	2.32	.023		

Table 27. Relation between transpiration rates per unit leaf area of sun and shade forms of various species when brought together in a given environment at the montane station.

1939								
Species	Source Station	In shade			In sun			
		S = Sh	S > Sh	S < Sh	S = Sh	S > Sh	S < Sh	
<i>Helianthus annuus</i> (RM)	M	x				x		
" (Can.)	M	x				x		
<i>Smilacina stellata</i>	M	x				x		
<i>Hieracium lanatum</i> (First)	P	x			x			
" "	M	x			x			
" "	A	x			x			
" (Second)	M	x			x			
<i>Mertensia sibirica</i> (First)	P	x				x		
" "	M	x			x			
" "	A	x			x			
" (Second)	A	x				x		
<i>Senecio aureus croceus</i>	M	x				x		
" cernuus	M		x		x			
" taraxacoides	A			x	x			
<i>Gum turbinatum</i>	P	x				x		
" "	M	x				x		
" "	A	x					x	
<i>Rubus strigosus</i>	M	x			x			
<i>Fragaria vesca</i>	M	x			x			
<i>virginiana</i>	M			x	x			
<i>Erigeron glabellus</i>	M	x			x			
<i>macranthus</i>	M			x	x			
<i>Solidago nana</i>	M		x			x		
" "	A	x				x		
" humilis	M				x			
<i>Mertensia alpina</i>	A	x			x			
<i>Potentilla hippiana</i>	M	x			x			
" nivea	A		x			x		
" rubricaulis	A		x			x		
<i>Primula angustifolia</i>	M-A	x			x			
<i>Tradescantia virginiana</i>	P	x			x			
1940								
<i>Mertensia sibirica</i>	M	x			x			
" "	A		x			x		
<i>Erigeron macranthus</i>	M	x				x		
<i>Potentilla rubricaulis</i>	A	x				x		
" nivea	A	x			x			
<i>Senecio cernuus</i>	M		x			x		
" taraxacoides	A	x			x			

P, M, and A stand for plains, montane, and alpine stations respectively. S means sun form and Sh shade form. Transpiration rates of the two forms are considered equal unless statistical tests show that the probability that the two values belong to the same population is equal to or less than 0.05.

## ADAPTATION AND ORIGIN IN THE PLANT WORLD

Table 28 . Data obtained in 1939 from short-period series with sun forms from climatically different stations.

Species	Series Location	Hours of series	Av. transpiration rate			Probability			No. of plants		
			P	M	A	P-M	P-A	M-A	P	M	A
<i>Helianthus annuus</i> (RM)	NH	55	1.45	1.41		.6			10	8	
	Sun	8	1.66	1.80		.28					
	Sun	17	0.275	0.347		<.01					
<i>Helianthus annuus</i> (Can.)	NH	55	1.44	1.40		.24			10	9	
	Sun	8	1.65	1.76		.08					
	Sun	17	0.308	0.332		<.01					
<i>Mertensia sibirica</i> (First series)	NH	55	1.80	1.07	1.17	.5		.7	2	4	5
	Shade	9	0.155	0.155	0.228			<.01			
	Sun	77	0.505	0.497	0.675			<.01			
<i>Mertensia sibirica</i> (Second series)	NH	5		2.17	0.49			<.01		8	5
	Shade	47		1.54	0.65			<.01			
	Sun	8		0.73	0.71			<.01			
<i>Heraclium lanatum</i> (First series)	NH	55	1.62	1.39	1.39	.44			6	5	6
	Shade	47	0.135	0.100	0.160			.28			
	Sun	77	0.533	0.511	0.749			.06			
<i>Senecio aureus croceus</i>	NH	7		5.60	3.07			<.01		9	10
	NH	24		2.06	1.13			<.01			
	Shade	40		0.358	0.424			.25			
<i>Senecio bigelovi</i>	NH	7		2.51	2.18			.12		10	9
	NH	24		1.02	0.92			.19			
	Shade	40		0.355	0.313			.11			
<i>Geum turbinatum</i>	NH	7	3.18	2.74	1.97	.06		<.01	8	8	8
	NH	24	1.31	1.28	0.84			<.01			
	Shade	40	0.598	0.424	0.518			.07			
<i>Solidago nana</i>	NH	6	1.88	1.80	0.77			<.01	10	6	10
	NH	5	2.09	2.03	0.93			<.01			
	Shade	47	0.32	0.56	0.65		.01	.05			
<i>Solidago humilis</i>	NH	6	3.39	2.06	0.68	.01		<.01	10	10	10
	NH	5	3.43	2.13	1.08			<.01			
	Shade	47	0.64	0.77	0.65			.1			
<i>Solidago missouriensis</i>	NH	6	4.26	2.84	0.50		.05	<.01	10	3	10
	NH	5	4.34	2.81	0.93		.01	<.01			
	Shade	47	0.84	0.89	0.97			.23			
<i>Potentilla rubricaulis</i>	NH	6	3.60		3.56		.01		10		10
	Shade	47	0.45		0.64			<.01			
	Sun	30	1.18		1.92						

P stands for plains, M for montane, and A for alpine stations. NH means native habitats, or the station at which the plants were grown. Probability means the chance that the two samples in question belong to the same population. Shade was furnished by a lath house.

Table 29 . Data obtained in 1940 from short-period series with sun forms from climatically different stations.

Species	Series Location	Hours of series	Av. transpiration rate		Probability	No. of plants
			M	A		
<i>Mertensia sibirica</i>	NH	5	0.66	0.82	.47	10
	Shade	49	0.554	0.541	.8	
	Sun	5	1.42	0.67	.01	
<i>Senecio bigelovi</i>	NH	5	1.69	2.10	.049	10
	Shade	45	0.214	0.296	<.01	
	Sun	6	1.51	2.61	<.01	
<i>Senecio aureus croceus</i>	NH	6	3.42	3.61	.78	9
	Shade	45	0.942	0.358	.06	
	Sun	6	2.46	2.19	.18	

M stands for montane and A for alpine stations. NH means native habitats, or the stations at which the plants were grown. Probability means the chance that the two samples in question belong to the same population. Shade was furnished by a lath house.

Table 30. Data obtained in 1940 from short-period series with shade forms from climatically different stations.

Species	Series Location	Hours of series	Av. transpiration rate		Probability M-A	No. of plants	
			M	A		M	A
<i>Mertensia sibirica</i>	NH	6	0.43	0.328	.06	9	10
	Shade	69	0.379	0.278	.01		
	Sun	5	1.74	0.79	.01		

M stands for montane and A for alpine stations. NH means native habitats, or the stations at which the plants were grown. Probability means the chance that the two samples in question belong to the same population. Shade was furnished by a lath house.

Table 31. Data obtained in 1939 from short-period series with shade forms from climatically different stations.

Species	Series Location	Hours of series	Av. transpiration rate			Probability			No. of plants		
			P	M	A	P-M	P-A	M-A	P	M	A
<i>Mertensia sibirica</i> (First series)	NH	56	0.73	0.59	0.83			.05	4	5	3
	Shade	48	0.142	0.127	0.284			.01			
	Sun	76	0.345	0.370	0.815			.01			
<i>Mertensia sibirica</i> (Second series)	NH	6		0.70	0.24			.01		5	5
	NH	5		0.63	0.27			.01			
	Shade	47		0.71	0.67			.12			
<i>Heracleum lanatum</i> (First series)	NH	56	1.04	0.54	0.72	.01	.01	.16	5	5	6
	Shade	48	0.149	0.126	0.156			.36			
	Sun	77	0.473	0.426	0.667			.03			
<i>Solidago nem.</i>	NH	6		0.90	1.47			.2	10		8
	NH	5		0.71	1.51			.02			
	Shade	47		0.46	0.78			.01			
<i>Geum turbinatum</i> (#5 cans)	Sun	8		1.89	4.16			.01			
	Sun	9		1.20	2.18			.01			
<i>Geum turbinatum</i> (#5 cans)	NH	7		1.43	1.47			.2	8		8
	NH	24		0.67	1.02			.04			
	Shade	40		0.484	0.629			.01			
<i>Geum turbinatum</i> (#2½ cans)	Sun	7		2.32	3.94			.15	5	5	8
	NH	24		0.83	1.16	.15	.17				
	Shade	40		0.417	0.700	.15	.2				
	Sun	7		2.32	3.94	.15	.2				

P stands for plains, M for montane, and A for alpine stations. NH means native habitats, or the stations at which the plants were grown. Probability means the chance that the two samples in question belong to the same population. Shade was furnished by a lath house.

Table 38. Relation between transpiration rates per unit leaf area of sun forms from climatically different stations when brought together in a given environment at the montane station.

In sun, 1939											
Species	P = M	P = M	P = M	M = A	M = A	M = A	P = A	P = A	A = P	A = P	A = P
<i>Helianthus annuus</i> (RM)			x								
" (Can.)			x								
<i>Mertensia sibirica</i> (First)	x					x					x
" (Second)											
<i>Horacleum lanatum</i>	x					x					x
<i>Potentilla rubricaulis</i>											x
<i>Senecio aureus croceus</i>				x							
" <i>bigelovi</i>						x					
<i>Geum turbinatum</i>	x			x			x				
<i>Solidago nana</i>	x					x					x
" <i>humilis</i>	x			x			x				
" <i>missouriensis</i>	x			x			x				
In sun, 1940											
<i>Mertensia sibirica</i>					x						
<i>Senecio aureus croceus</i>				x							
" <i>bigelovi</i>						x					
In shade, 1939											
<i>Mertensia sibirica</i> (First)	x					x					x
" (Second)				x							
<i>Horacleum lanatum</i>	x			x			x				
<i>Senecio aureus croceus</i>				x							
" <i>bigelovi</i>				x							
<i>Geum turbinatum</i>	x			x			x				
<i>Solidago nana</i>			x	x							x
" <i>humilis</i>	x			x			x				
" <i>missouriensis</i>	x			x			x				
<i>Potentilla rubricaulis</i>											x
In shade, 1940											
<i>Mertensia sibirica</i>				x							
<i>Senecio aureus croceus</i>				x							
" <i>bigelovi</i>						x					

P, M, and A stand for plains, montane, and alpine stations respectively. The transpiration rates of the two forms compared are considered equal unless statistical tests show that the probability that the two values belong to the same population is equal to or less than 0.05.

Table 33. Relation between transpiration rates per unit leaf area of shade forms from climatically different stations when brought together in a given environment at the montane station.

In sun, 1939											
Species	P = M	P	M	P	M	M = A	M	A	M	A	P = A
<i>Mertensia sibirica</i> (First)	x								x		
" (Second)						x					x
<i>Heracleum lanatum</i>	x								x		
<i>Solidago nana</i>									x		
<i>Geum turbinatum</i> (#5 cans)									x		
" (#2)	x					x				x	
In sun, 1940											
<i>Mertensia sibirica</i>								x			
In shade, 1939											
<i>Mertensia sibirica</i> (First)	x								x		
" (Second)						x					x
<i>Heracleum lanatum</i>	x									x	
<i>Solidago nana</i>									x		
<i>Geum turbinatum</i> (#5 cans)									x		
" (#2)	x					x				x	
In shade, 1940											
<i>Mertensia sibirica</i>								x			

P, M, and A stand for plains, montane, and alpine respectively. The rates of transpiration of the two forms compared are considered equal unless statistical tests show that the probability that the two values belong to the same population is equal to or less than 0.05.

Table 34. Transpiration rates per unit leaf area of various species expressed in percentage of that of *Helianthus annuus*.

Species	Source	In sun	In shade
<i>Senecio cernuus</i>	Montane sun	65	101
" <i>bigelovi</i>	Montane sun	41	60
" "	Alpine sun(native)	70	82
" <i>aureus croceus</i>	Montane sun	66	67
" <i>taraxacoides</i>	Alpine sun	55	90
" <i>fendleri</i>	Montane sun	75*	78*
" <i>oblongeolatus</i>	Plains sun	90*	105*
<i>Mertensia sibirica</i>	Montane sun	50*	61
" "	Alpine sun(native)	29*	63
" <i>viridus</i>	Montane shade	35*	65*
" <i>alpina</i>	Alpine sun	72*	81*
<i>Erigeron macranthus</i>	Montane sun	48	61
" <i>glabellus</i>	Montane shade	55*	61*
<i>Potentilla gracilis</i>	Montane sun	95	98
" <i>nivea</i>	Alpine sun	70	96
" <i>rubricaulis</i>	Alpine sun	84	113
" <i>hippiana</i>	Montane sun	70*	82*
<i>Solidago nana</i>	Alpine sun	64	56
" <i>humilis</i>	Montane sun	55*	64*
" <i>missouriensis</i>	Montane sun	53*	72*
<i>Fragaria virginiana</i>	Montane shade	52	83
" <i>vesca</i>	Montane sun	58*	115*
<i>Rubus strigosus</i>	Montane sun	21	21
<i>Geum turbinatum</i>	Alpine sun	46	69
<i>Heracleum lanatum</i>	Montane sun	50*	61*
<i>Primula angustifolia</i>	Alpine sun	76*	100*

\* These values obtained by comparing series in 1939 with those in 1940. Other values obtained by direct comparison with *Helianthus annuus* phytometers.

Table 35. Stomatal frequency and dimensions for various species used as phytometers in 1939.

Species	Source	Upper epidermis			Lower epidermis		
		No. mm <sup>2</sup>	Dimen- sions	LSO	No. mm <sup>2</sup>	Dimen- sions	LSO
<i>Helianthus annuus</i> (Can.)	Flains sun	307	21 x 30	14	309	21 x 31	17
	Montane sun	223	21 x 34	13	355	22 x 29	15
	Montane shade	58	21 x 31	12	117	24 x 30	14
<i>Helianthus annuus</i> (RM)	Flains sun	172	18 x 29	16	283	21 x 28	11
	Montane sun	193	19 x 30	14	286	18 x 27	13
	Montane shade	74	18 x 30	13	122	21 x 30	17
<i>Smilicina stellata</i>	Montane sun	0			80	36 x 40	18
	Montane shade	0			86	32 x 36	14
<i>Senecio fendleri</i>	Montane sun	70	32 x 22	13	149	28 x 21	11
" <i>oblancoelatus</i>	Flains sun	125	33 x 23	15	196	29 x 22	13
" <i>bigelovi</i>	Alpine sun	68	48 x 35	20	83	39 x 32	13
"	Montane sun	24	46 x 34	21	71	48 x 25	22
<i>Senecio aureus croceus</i>	Montane sun	63	29 x 26	12	86	31 x 25	12
	Montane shade	97	34 x 22	11	131	30 x 26	12
	Alpine sun	100	34 x 28	10	232	32 x 26	10
<i>Senecio taraxacoides</i>	Alpine sun	89	44 x 37	18	108	41 x 33	15
<i>Senecio cernuus</i>	Alpine shade	24	43 x 36	22	41	41 x 35	18
	Montane sun	59	45 x 39	21	105	46 x 38	19
	Montane shade	31	46 x 33	21	60	46 x 32	24
<i>Geum turbinatum</i>	Flains sun 3	100	30 x 21	10	115	30 x 22	12
	Flains shade 2½	110	29 x 20	9	71	30 x 22	12
	Montane sun 3	128	29 x 20	9	80	32 x 21	12
	Montane shade 3	78	32 x 25	10	59	34 x 25	11
	Montane shade 2½	98	32 x 21	13	70	31 x 21	10
	Alpine sun 3	165	31 x 23	10	108	32 x 21	15
	Alpine shade 3	110	32 x 27	10	63	29 x 22	8
	Alpine shade 2½	119	30 x 23	8	84	33 x 22	12
<i>Erigeron glabellus</i>	Montane sun	41	32 x 24	12	38	34 x 24	13
	Montane shade	31	34 x 23	15	45	37 x 32	12
<i>Erigeron macranthus</i>	Montane sun	142	25 x 21	9	194	25 x 21	9
	Montane shade	90	25 x 21	9	88	25 x 21	9
<i>Fragaria virginiana</i>	Montane sun	9	30 x 25	11	143	26 x 20	11
	Montane shade	0			101	26 x 20	11
<i>Fragaria vesca</i>	Montane sun	0			91	23 x 17	10
	Montane shade	0			142	23 x 17	8
<i>Rubus strigosus</i>	Montane sun	0				Too hairy	
	Montane shade	0					
<i>Mertensia sibirica</i> (First series)	Flains sun	0			347	22 x 12	8
	Flains shade	0			212	23 x 17	8
	Montane sun	0			248	20 x 16	7
	Montane shade	0			267	21 x 15	8
	Alpine sun	0			257	23 x 19	7
	Alpine shade	0			293	22 x 18	7
<i>Mertensia sibirica</i> (Second series)	Montane sun	16	29 x 20	14	221	27 x 18	13
	Montane shade	12	22 x 17	10	146	22 x 15	9
	Alpine sun	1	28 x 19	8	236	25 x 17	10
	Alpine shade	0			200	25 x 16	9

Table 35 (Cont.). Stomatal frequency and dimensions for various species used as phytometers in 1939.

Species	Source	Upper epidermis			Lower epidermis		
		No. mm <sup>2</sup>	Dimen- sions	LSO	No. mm <sup>2</sup>	Dimen- sions	LSO
<i>Mertensia viridus</i>	Montane shade	28	27 x 21	12	84	25 x 19	12
"	Alpine sun	145	30 x 20	12	117	27 x 22	11
"	Alpine shade	78	28 x 18	10	68	30 x 20	12
<i>Primula angustifolia</i>	Montane shade	45	43 x 33	20	40	48 x 37	21
"	Alpine sun	82	40 x 33	19	56	45 x 35	20
<i>Tradescantia virginiana</i>	Plains sun	14	60 x 41	27	27	63 x 37	32
"	Plains shade	18	62 x 37	38	23	67 x 27	42
<i>Hieracium lanatum</i> (Second series)	Montane sun	2	31 x 23	15	232	28 x 18	12
"	Montane shade	6	34 x 22	16	140	29 x 19	12
<i>Solidago nana</i>	Plains sun	92	31 x 25	13	72	31 x 25	15
"	Montane sun	71	34 x 28	18	72	33 x 28	18
"	Montane shade	66	31 x 26	16	40	32 x 27	15
"	Alpine sun	116	31 x 27	14	93	31 x 25	13
"	Alpine shade	82	33 x 24	15	59	34 x 27	18
<i>Solidago humilis</i>	Plains sun	84	32 x 26	16	54	32 x 25	17
"	Montane sun	74	32 x 25	17	83	30 x 25	17
"	Montane shade	56	30 x 21	15	54	32 x 23	18
"	Alpine sun	79	32 x 24	17	75	33 x 25	16
<i>Solidago missouriensis</i>	Plains sun	79	37 x 27	20	68	37 x 28	19
"	Montane sun	54	40 x 26	20	54	41 x 32	23
"	Alpine sun	74	32 x 23	16	75	33 x 24	18
<i>Potentilla rubricaulis</i>	Plains sun	0				Too hairy	
"	Alpine sun	26	30 x 26	12			
"	Alpine shade	5	27 x 23	11	143	25 x 21	9
<i>Potentilla nives</i>	Alpine sun	50	32 x 22	18	114	31 x 23	15
"	Alpine shade	32	33 x 26	15	95	30 x 21	14
<i>Potentilla gracilis</i>	Montane sun	0			219	27 x 21	13
<i>Potentilla hippiana</i>	Montane sun	0				Too hairy	
"	Montane shade	0					

LSO stands for the length of a stomatal opening. Dimensions are the length and width of a stoma, including both guard cells. All measurements are in microns. Can. means Canadian variety, S-490, and RM means Russian Mammoth variety. The numbers 5 and 23 following the source name for *Geum turbinatum* represent the size number of the cans in which they were grown.



Table 36 . Measurements made from sections of leaves of various species used as phytometers in 1939 and 1940.

Species	Source	Total leaf	Upper epidermis		Lower epidermis		Pali- sade	RLA	
			Total	Cuticle	Total	Cuticle			
<i>Helianthus annuus</i> (Can)	Plains sun	306	18	4	14	3	51(2)	4	
	Montane sun	357	18	4	14	3	53(2)	3	
	Montane shade	238	11	2	7	2	31(1)	1	
<i>Helianthus annuus</i> (RM)	Plains sun	374	18	4	14	3	51(2)	4	
	Montane sun	357	18	4	14	3	53(2)	3	
	Montane shade	238	11	2	7	2	35(1)	1	
<i>Smilicina stellata</i>	Montane sun	315	46	4	34	4	--	1 1/2	
	Montane shade	225	46	4	34	4	--	1 1/2	
<i>Senecio fendleri</i> " <i>oblanceolatus</i>	Montane sun	442	35	5	21	5	58		
	Plains sun	544	46	12	35	11	100		
<i>Senecio bigelovi</i>	Montane sun	570	39	5	39	5	46(2)	6	
	Alpine sun	570	42	7	35	7	46(2)	1	
<i>Senecio aureus croceus</i>	Montane sun	544	21	5	21	5	36(2)	2	
	Montane shade	289	18	4	18	4	29(1)	3 1/2	
	Alpine sun	374	18	5	18	5	38(2)	1	
<i>Senecio taraxacoides</i>	Alpine sun	850	35	7	35	5	100	1	
	Alpine shade	493	43	4	28	4	43(2)	2 1/2	
<i>Senecio cernuus</i>	Montane sun	595	43	11	32	11	46(2)	1	
	Montane shade	442	46	7	35	7	21(1 1/2)	2	
<i>Geum turbinatum</i>	Plains sun	408	25	5	25	5	45(2)	1	
	Plains shade	204	18	4	18	4	50(2)	1	
	Montane sun	272	18	4	18	4	38(2)	1 1/2	
	Montane shade	221	18	4	18	4	45(2)	2	
	Alpine sun	340	16	4	16	4	43(2)	1	
	Alpine shade	221	18	2	14	2	38(2)	1	
<i>Erigeron glabellus</i>	Montane sun	272	21	4	14	4	29(1)	1	
	Montane shade	272	No difference detectable						1 1/2
<i>Erigeron macranthus</i>	Montane sun	225	18	2	18	2	100(5)	1	
	Montane shade	180	18	2	18	2	38(1 1/2)	1 1/2	
<i>Fragaria virginiana</i>	Montane sun	187	28	5	14	4	58(2)	1	
	Montane shade	136	21	4	11	3	36(1)	1 1/2	
<i>Fragaria vesca</i>	Montane sun	204	25	7	14	4	46(2)	2	
	Montane shade	170	21	4	14	4	44(2)	1	
<i>Rubus strigosus</i>	Montane sun	119	14	4	14	2	62(2)	1	
	Montane shade	85	11	1	11	1	35(1)	1	
<i>Mertensia sibirica</i> (First series)	Plains sun	374	21	7	21	7	28		
	Plains shade	238	18	5	14	5	25		
	Montane sun	255	21	5	18	5	26		
	Montane shade	289	18	4	14	4	17		
	Alpine sun	306	28	7	18	5	21		
	Alpine shade	357	21	7	18	5	19		
<i>Mertensia sibirica</i> (Second series)	Montane sun	425	28	4	28	4	29(1)	3	
	Montane shade	Leaves too	delicate to section						2
	Alpine sun	340	28	4	18	4	25(1)	1	
	Alpine shade	Leaves too	delicate to section						3

Table 36 (Cont.). Measurements made from sections of leaves of various species used as phytometers in 1959 and 1940.

Species	Source	Total leaf	Upper epidermis		Lower epidermis		Palisade	RLA
			Total	Cuticle	Total	Cuticle		
<i>Mertensia viridus</i> " <i>alpina</i>	Montane shade	187	28	3	21	3	40(1)	
	Alpine sun	272	21	7	21	7	62(3)	1
	Alpine shade	272	21	4	21	4	43(3)	3
<i>Primula angustifolia</i>	Montane shade	340	35	4	28	4	39(2)	2
	Alpine sun	510	35	5	35	5	41(3)	1
<i>Tradescantia virginiana</i>	Plains sun	510	57	5	46	5		
	Plains shade	561	57	5	46	5		
<i>Hieracium lanatum</i> (Second series)	Montane sun	170	18	2	18	2	55(1)	1
	Montane shade	221	18	2	18	2	41(1)	1
<i>Solidago nana</i>	Plains sun	340	28	9	25	7	100	4
	Montane sun	340	32	9	28	7	100	6
	Montane shade	238	25	4	25	4	29(2)	4
	Alpine sun	340	35	9	28	9	100	1
	Alpine shade	221	21	4	21	4	31(2)	1
<i>Solidago humilis</i>	Plains sun	391	28	9	25	9	100	3
	Montane sun	340	25	7	25	7	100	1
	Montane shade	221	21	4	21	4	37(2)	4
	Alpine sun	272	21	5	21	5	100	1
<i>Solidago missouriensis</i>	Plains sun	340	28	5	25	5	100	2
	Montane sun	289	25	7	25	7	100	1
	Alpine sun	289	25	7	28	9	32(2)	1
<i>Potentilla rubricaulis</i>	Plains sun	238	28	5	21	4	55(3)	1
	Alpine sun	170	28	7	18	3	62(3)	1
	Alpine shade	221	35	4	28	4	47(2)	1
<i>Potentilla nivea</i>	Alpine sun	221	43	4	28	4	50(2)	1
	Alpine shade	255	35	4	21	4	46(2)	1
<i>Potentilla hippiana</i>	Montane sun	187	28	4	14	2	51(3)	1
	Montane shade	153	21	3	14	3	57(2)	1
<i>Potentilla gracilis</i>	Montane sun	204	21	3	18	2	66(2)	

Thicknesses of leaf, epidermis, and cuticle are given in microns. The palisade is expressed in percentage of the mesophyll thickness, and the number of layers of palisade cells is given in parentheses. The leaf area is given in relative values (RLA), which hold only within the species for which they are given and bear no relation to other species. Can. means Canadian variety S-490, and RM means Russian Mammoth variety.

Table 37 . Relative transpiration rates of sun and shade forms of several montane species obtained from short-period measurements with detached leaves and shoots. Comparisons were made in shade, and each value given is the average of four independent runs.

Species	Short-period interval no.	
	1	2
<i>Senecio bigelovi</i> (alpine form)	1.62	1.57
" (subalpine form)	2.25	1.58
<i>Erigeron subtrinervis</i>	1.62	2.13
<i>Rubus strigosus</i>	1.03	1.30
<i>Rudbeckia hirta</i>	0.56	0.53
<i>Monarda fistulosa</i>	1.11	1.29
<i>Prunus demissa</i>	1.28	1.39

Table 38 . Osmotic concentration in atmospheres of expressed sap of leaves of various species. Samples taken on August 18, 1938.

Species	Station	Habitat	Ov
<i>Geum turbinatum</i>	Montane	Lath house	15.3
		Moist sun	16.8
	Alpine	Slag pile	19.3
<i>Agropyrum scribberii</i>	Montane	Lath house	13.6
		Wet sun	17.0
	Alpine	Climax soil pit	16.8
		Gopher mound soil pit	18.1
		Sand soil pit	17.0
		Adobe soil pit	15.9
<i>Iris missouriensis</i>	Montane	Lath house	12.8
		Moist sun	15.7
		Wet sun (by pool)	15.7
<i>Rudbeckia hirta</i>	Montane	Lath house	9.6
		Wet sun (by pool)	11.5
<i>Rubus strigosus</i>	Montane	Lath house	12.3
		Dry sun	15.3
		Wet sun (by pool)	16.2
<i>Mertensia alpina</i>	Montane	Wet sun	11.5
	Alpine	Climax	11.5
		Gopher mound	11.5
<i>Mertensia sibirica</i>	Montane	Lath house	9.9
		Wet shade	10.1
		Wet sun	14.1
	Alpine	Wet sun (by pool)	11.9
		Moist sun	9.9
		Lath house 20%	8.4
		Lath house 10%	7.5
<i>Smilacina stellata</i>	Montane	Lath house	9.6
		Moist sun	14.3
<i>Senecio fremonti</i>	Alpine	Dry sun	9.9
		Lath house 20%	7.9
		Lath house 10%	6.5
<i>Polygonum bistorta</i>	Alpine	Climax soil pit	11.2
		Gopher mound soil pit	9.2
		Sand soil pit	8.9
		Adobe soil pit	10.7

Samples were taken on a day when the sky was clear, and evaporating conditions were good. Samples were collected at the Montane station between 12:30 PM and 2:00 PM, and those at the Alpine station between 1:00 PM and 4:00 PM. Ov values were probably about the maximum for the day.

## TABLES

301

Table 39 . Osmotic concentration in atmospheres of expressed sap of leaves of various species. Samples taken August 19, 1938.

Species	Station	Habitat	Ov
<i>Geum turbinatum</i>	Montane	Lath house	13.5
		Moist sun	16.0
<i>Agropyrum scribneri</i>	Montane	Lath house	13.2
		Wet sun	14.6
<i>Iris missouriensis</i>	Montane	Lath house	11.1
		Moist sun	13.1
		Wet sun(by pool)	13.1
<i>Rudbeckia hirta</i>	Montane	Lath house	10.3
		Wet sun(by pool)	11.2
<i>Rubus strigosus</i>	Montane	Lath house	10.3
		Dry sun	12.0
		Wet sun(by pool)	14.0
<i>Mertensia alpina</i>	Montane	Wet sun	10.5
<i>Mertensia sibirica</i>	Montane	Lath house	9.5
		Wet shade	9.5
		Wet sun	12.3
<i>Smilicina stellata</i>	Montane	Lath house	8.3
		Moist sun	11.1

Collecting time between 5:10 AM and 5:50 AM, before sunrise. These Ov values are probably about the minimum for the day. These were taken to compare with the values in table to show the diurnal variation in these species.

Table 40 . Osmotic concentration in atmospheres of expressed sap of leaves of various species. Samples taken on July 18, 1939.

Species	Station	Habitat	Ov
<i>Solidago missouriensis</i>	Montane	Dry sun	14.9
		Moist sun	13.5
<i>Solidago humilis</i>	Montane	Dry shade	24.7
		Moist sun	13.1
		Moist shade	13.0
<i>Solidago nemoralis</i>	Montane	Moist sun	12.4
		Moist shade	11.5
<i>Solidago speciosa</i>	Montane	Moist sun	10.9
		Moist shade	9.6
<i>Smilicina stellata</i>	Montane	Dry sun	13.6
		Dry shade	10.9
<i>Senecio fendleri</i>	Montane	Dry sun	18.9
		Moist sun	10.7
		Moist shade	9.5
<i>Senecio cernuus</i>	Montane	Dry shade	21.8
		Moist sun	12.6
		Moist shade	10.5
<i>Senecio bigelovi</i>	Montane	Moist sun	10.0
		Moist shade	8.4
<i>Rubus strigosus</i>	Montane	Wet sun	15.7
		Dry sun	15.7
		Moist shade	15.2
<i>Mertensia sibirica</i>	Montane	Wet sun	11.2
		Wet shade	9.7
		Moist sun	9.7
<i>Mertensia viridis</i>	Montane	Dry shade	19.4
		Moist sun	13.6
<i>Erigeron glabellus</i>	Montane	Dry shade	14.2
		Moist sun	12.4
		Moist shade	9.9
<i>Erigeron viscidus</i>	Montane	Moist sun	12.5
		Moist shade	11.2
<i>Erigeron macranthus</i>	Montane	Moist sun	14.6
		Moist shade	12.5

Samples were collected 8:00 AM and 11:15 AM. Many of these species in their native habitats were suffering from lack of water due to a prolonged drought. Some were wilted and about to lose their leaves.

Table 41. Osmotic concentration in atmospheres of expressed sap of leaves of various species. Samples taken on August 10, 1939.

Species	Station	Habitat	Ov
<i>Mertensia sibirica</i>	Montane	Wet sun	10.9
		Wet shade	7.1
		Lath house	10.3
		Moist sun	10.5
	Alpine	Wet sun(by pool)	11.5
		Moist sun	13.7
		Lath house 20%	9.1
<i>Agropyrum sibiricum</i>	Plains	Moist sun	16.4
	Montane	Wet sun	15.7
		Lath house	14.0
	Alpine	Gopher mound	19.4
		Slag pile	18.7
<i>Polygonum bistorta</i>	Plains	Wet sun	10.2
	Montane	Dry sun	11.1
		Wet sun	8.6
	Alpine	Wet sun(by pool)	8.8
		Gopher mound	11.0
<i>Mertensia alpina</i>	Montane	Wet sun	11.7
	Alpine	Gopher mound	14.0
<i>Geum turbinatum</i>	Plains	Wet sun	16.3
	Montane	Dry sun	15.1
		Moist sun	18.6
		Wet sun	15.9
		Lath house	14.8
		Gopher mound	20.4
	Alpine	Slag pile	19.9
		Sublimax	20.5
		Wet sun(by pool)	17.9

Samples taken between 10:00 AM and 1:00 PM.

Table #2 . Osmotic concentration in atmospheres of expressed sap of leaves of various species. Samples taken August 29, 1939.

Species	Station	Habitat	Ov
<i>Solidago nana</i>	Flains	Wet sun	13.9
		Dry sun	16.5
	Montane	Moist sun	12.3
		Wet sun	14.3
	Alpine	Moist shade	9.8
		Moist sun	14.4
<i>Solidago nemoralis</i>	Flains	Moist sun	14.0
	Montane	Moist sun	13.2
		Wet sun	12.8
		Moist shade	11.1
		Dry sun	12.8
	Alpine	Moist sun	13.7
<i>Geum turbinatum</i>	Flains	Wet sun	17.5
	Montane	Dry sun	18.9
		Moist sun	18.5
	Alpine	Moist shade	13.2
		Gopher mound	18.6
		Wet sun(by pool)	17.8
<i>Achillea m. alpina</i>	Flains	Wet sun	13.4
		Dry sun	15.1
	Montane	Wet sun	12.5
	Alpine	Slag pile	15.4
<i>Potentilla rubricaulis</i>	Flains	Wet sun	15.3
	Montane	Dry sun	17.0
		Wet sun	14.0
	Alpine	Subclimax	18.1
<i>Agropyrum scribneri</i>	Flains	Moist sun	16.3
	Montane	Wet sun	15.8
	Alpine	Gopher mound	18.5
		Slag pile	17.8
<i>Polygonum bistorta</i>	Flains	Wet sun	10.1
	Alpine	Gopher mound	10.9
		Wet sun(by pool)	9.8
		Lath house 20%	8.9
<i>Senecio aureus croceus</i>	Montane	Moist sun	12.0
	Alpine	Moist sun	14.0
<i>Senecio bigelovi</i> (Subalpine form) <i>Senecio bigelovi</i> (Timberline form)	Montane	Moist sun	10.8
	Montane	Moist shade	8.9
		Moist shade	9.4
		Wet sun	11.4
	Alpine	Timberline(Moist sun)	10.5
<i>Senecio cernuus</i>	Montane	Moist sun	14.3
		Moist shade	10.6

Samples were taken between 9:00 AM and 10:00 AM at the plains, between 10:00 AM and 1:00 PM at the montane station, and between 1:00 PM and 3:00 PM at the alpine station.

Table 43. Atmospheric factor data at times of collection of samples for the osmotic concentration values given in tables .

Date	Station	Habitat	Time	Air Temp.	Rel. Hum.	Approx. Wind	Condition of sky
				°F	%	mph	
8/18/38	Montane	Dry sun	1:00 PM	80	22	5-10	Clear
		Moist sun	1:30 PM	76	24	5-10	"
		Wet sun	1:15 PM	76	28	5-10	"
		Wet shade	2:00 PM	69	34	0-2	"
	Alpine	Lath house	12:30 PM	74	25	0-1	"
		Climax	4:00 PM	58	30	10-15	"
		Gopher mound	1:00 PM	66	21	10-15	"
		Wet sun (by pool)	3:00 PM	60	41	10-15	"
		Moist sun	2:00 PM	62	34	10-15	"
		Slag pile	2:30 PM	62	33	10-15	"
		Lath house 20%	4:00 PM	56	38	0-2	"
		Lath house 10%	3:45 PM	55	41	0-2	"
8/19/38	Montane	All	5:30 AM	48	50	0-1	Clear
7/18/39	Montane	Dry sun	8:00 AM	70	29	3-5	Clear
		Wet sun	9:00 AM	74	24	3-5	"
		Wet shade	9:15 AM	73	26	0-1	"
		Dry shade	9:30 AM	73	23	0-1	"
		Moist sun	10:00 AM	70	26	0-1	"
		Moist shade	10:45 AM	74	24	0-1	"
8/10/39	Plains	Sun	11:00 AM	68	41	10-15	Few cumuli
	Montane	Wet sun	10:15 AM	64	56	2-5	"
		Lath house	10:40 AM	61	60	0-1	"
		Moist sun	11:00 AM	66	57	2-5	"
	Alpine	Wet sun	12:45 PM	62	59	5-10	"
		Wet shade	1:10 PM	60	59	0-3	"
		Wet sun	11:00 AM	56	48	5-10	Clear
		Moist sun	11:10 AM	63	43	0-3	"
		Slag pile	11:15 AM	55	42	5-10	"
		Gopher mound	11:30 AM	58	42	10-15	"
		Subclimax	11:35 AM	58	45	10-15	"
		Lath house 20%	11:50 AM	55	48	0-2	"
8/29/39		Plains	Sun	9:00 AM	78	38	1-5
	Montane	10:00 AM	83	31	1-5	"	
		Dry sun	1:10 PM	73	44	0-3	"
		Wet sun	12:45 PM	70	46	0-3	"
	Alpine	Moist sun	10:00 AM	69	43	0-3	"
		Moist shade	10:45 AM	69	45	0-3	"
		Climax	1:15 PM	57	58	5	"
		Slag pile	3:00 PM	57	58	5	"
		Timberline	3:15 PM	58	59	5	"

## TABLES

305

Table 44. Final measurements of plants of *Helianthus annuus* grown in soil pits at the plains, montane, and alpine stations during the summer of 1956. Measurements taken August 31.

Station	Habitat	Soil	Leaf Area cm <sup>2</sup>	No. of Leaves	Stem height cm	Stem diam. cm	Fresh weight gm	Dry weight gm	Per cent. water	No. of plants	Height Diameter	Height Dry weight
Plains	Sun	Imp.	264	43	166	3.26	2199	245	81.2	6	50.6	0.67
		Nat.	144	40	102	1.96	886	130	86.3	3	52.0	0.78
	Lath house	Imp.	7.13	13	109	0.54	31.3	2.77	91.2	8	202	39.4
		Nat.	0.60	18	116	0.63	46.5	3.83	91.8	3	184	30.2
	Lath house	Imp.	7.53	15	112	0.65	29.4	2.42	91.8	10	204	46.2
		Nat.	7.11	13	116	0.49	27.1	2.12	92.2	7	237	54.7
Montane	Dry sun	Imp.	86.0	31	123	2.17	551	72.6	86.8	10	56.7	1.69
		Nat.	40.3	27	94	1.68	227	25.5	88.8	10	59.5	3.68
	Moist sun	Imp.	70.7	32	105	2.11	462	61.5	86.7	10	49.7	1.70
		Nat.	19.7	23	62	1.08	84	11.1	86.7	10	56.8	5.58
	Lath house	Imp.	12.2	16	107	0.85	45.8	4.55	91.1	8	125	23.2
		Nat.	5.4	15	84	0.55	18.9	1.82	89.9	10	183	46.2
	Dry shade	Imp.	7.60	15	92	0.79	37.7	2.26	94.0	10	117	40.7
		Nat.	4.83	13	70	0.62	19.2	1.69	92.0	10	113	44.0
	Moist shade	Imp.	1.86	10	46	0.36	5.35	0.38	92.9	9	129	122
		Nat.	1.80	10	40	0.31	3.61	0.38	89.4	8	130	107
Alpine	Climax	Imp.	2.25	12	19	0.51	11.1	1.37	87.6	12	37.0	13.8
		Nat.	0.43	6	12	0.37	2.83	0.52	81.6	12	31.1	22.1
	Sub-climax	Imp.	3.75	12	21	0.62	17.0	1.83	89.2	12	34.0	11.5
		Nat.	0.72	7	13	0.37	4.33	0.73	83.1	12	34.3	17.4
	Gopher mound	Imp.	2.19	12	18	0.52	10.7	1.38	87.1	12	35.4	15.3
		Nat.	0.67	8	14	0.39	4.33	0.60	86.1	6	34.9	22.7
	Slag pile	Imp.	3.72	14	25	0.60	16.7	2.15	87.1	12	40.8	11.3
		Nat.	0.96	10	15	0.40	5.60	0.74	86.5	12	37.0	20.0
	Lath house	Imp.	0.64	5	20	0.32	2.93	0.36	87.7	11	61.2	54.5
		Nat.	0.51	5	21	0.30	2.92	0.40	86.3	12	70.0	52.5
	Lath house	Imp.	0.69	5	21	0.31	2.90	0.34	88.3	10	67.1	61.3
		Nat.	0.58	5	21	0.29	2.58	0.35	86.4	12	70.6	58.6

Imp. = imported soil, Nat. = native soil.

Table 45. Final measurements of plants of *Helianthus annuus* grown in soil pits at the plains, montane, and alpine stations during the summer of 1957. Measurements taken August 30.

Station	Habitat	Soil	Leaf Area cm <sup>2</sup>	No. of Leaves	Stem height cm	Stem diam. cm	Fresh weight gm	Dry weight gm	Per cent. water	No. of plants	Height Diameter	Height Dry weight
Plains	Sun	Imp.	332	35	174	2.98	1701	275	83.8	9	58.4	0.61
		Nat.	122	36	126	1.85	691	107	84.5	10	69.2	1.20
	Lath house	Imp.	9.3	16	129	0.57	34.7	3.08	91.1	6	226	41.8
Montane	Dry sun	Imp.	60.8	32	164	2.00	555	88.9	84.0	10	82.0	1.84
		Nat.	45.6	31	138	1.60	373	59.4	84.2	10	86.2	2.32
	Moist sun	Imp.	58.9	36	150	1.85	473	84.1	82.2	10	81.0	1.78
		Nat.	12.1	23	86	0.98	81.4	12.2	85.1	10	87.7	7.05
	Lath house	Imp.	28.5	25	179	1.20	137	12.2	91.1	9	149	14.7
		Nat.	12.3	21	156	0.79	66.3	6.2	90.7	10	198	25.2
	Dry shade	Imp.	12.1	19	127	0.77	66.7	4.63	93.1	9	165	27.4
		Nat.	9.4	19	128	0.77	56.5	4.44	92.2	7	166	28.8
	Moist shade	Imp.	2.5	13	62	0.37	7.77	0.85	92.9	9	168	112
		Nat.	2.4	12	71	0.36	7.12	0.48	93.3	10	197	148
Alpine	Climax	Imp.	5.44	16	31.6	0.78	25.0	3.74	85.0	10	41.6	8.46
		Nat.	2.79	13	28.3	0.65	14.6	2.48	88.0	10	45.0	11.4
	Sub-climax	Imp.	6.02	16	34.2	0.77	27.4	4.31	84.3	10	44.4	7.94
		Nat.	3.16	14	27.8	0.66	15.9	3.02	81.0	10	42.1	9.21
	Gopher mound	Imp.	4.90	17	33.0	0.73	29.0	3.97	86.3	2	45.3	8.30
		Nat.	2.70	13	28.2	0.62	13.9	2.45	82.4	8	45.4	11.6
	Slag pile	Imp.	7.25	16	34.5	0.82	32.5	4.93	84.8	7	48.0	7.0
		Nat.	3.02	12	28.5	0.65	17.7	2.68	84.8	10	45.9	10.6
	Lath house	Imp.	2.06	10	42.5	0.44	8.27	0.96	89.3	10	97	44.3
		Nat.	1.70	9	40.1	0.41	7.57	0.91	87.6	10	98	44.1
	Lath house	Imp.	2.68	10	42.9	0.47	9.36	1.01	89.2	10	91	42.5
		Nat.	1.15	8	39.1	0.43	6.90	0.82	88.1	9	91	47.7

Imp. = imported, and Nat. = native.



Table 46. Results of two series of free phytometers of *Helianthus annuus* for a comparison of mean growth rates in various habitats. Both series were run in the summer of 1939.

Series	Station	Habitat	Final leaf area dm <sup>2</sup>	Final dry weight gm	Mean growth rate gm/dm <sup>2</sup> /week
I	Plains	Dry sun	30.5	35.7	0.266
	Montane	Wet sun	48.1	45.8	0.367
		Dry sun	25.6	16.1	0.249
		Wet sun	8.74	4.50	0.216
		Lath house 20%	0.87	0.360	0.079
II	Plains	Dry sun	2.12	0.99	0.330
	Montane	Wet sun	8.38	2.98	0.352
		Dry sun	1.32	0.516	0.185
		Moist sun	3.14	0.958	0.247
		Wet sun	1.07	0.325	0.104
		Moist shade	0.452	0.125	0.053

The first series ran for seven weeks, the second for three.

Table 47. Frequency and dimensions of stomata of transplants in the adaptation gardens in Colorado. The outside dimensions of the guard cells and length of stomatal opening (LSO) are both in microns.

Species	Habitat	Stake Label	Upper epidermis			Lower epidermis			Leaf dimensions			Relative leaf area
			No. mm <sup>2</sup>	Dimen- sions	LSO	No. mm <sup>2</sup>	Dimen- sions	LSO	Length	Width	Area	
<i>Agropyrum violaceum</i>	Alpine sun	3832	92	59 x 24	24	63	50 x 35	16	14.4	0.7	7.7	1.1
	Alpine lath house	3822	35	63 x 27	24	22	55 x 31	20	15.0	0.5	6.8	1
<i>Bromus inermis</i>	Montane dry sun	3854	86	51 x 27	16	50	47 x 31	16	10.6	0.7	8.1	1.1
	moist sun #2	3764	78	55 x 27	20	34	59 x 27	20	18.4	0.8	9.9	1.4
	moist sun #3	3854	49	55 x 27	20	30	51 x 31	18	26.0	1.0	15.3	2.4
	moist sun #3	40584	72	51 x 31	27	46	55 x 31	24	18.0	0.9	12.5	1.7
	wet sun #6	3854	59	55 x 27	20	52	51 x 27	20	15.8	0.65	7.2	1.0
	moist shade	3854	87	51 x 27	20	46	51 x 27	20	25.0	0.7	12.5	1.6
	lath house #3	3854	52	51 x 27	20	29	51 x 35	16	23.0	0.65	10.9	1.5
	Alpine sun	3782	65	55 x 27	20	72	55 x 27	24	14.0	0.8	8.5	1.2
<i>Bromus pumellianus</i>	Alpine sun	3832	46	63 x 43	24	45	63 x 39	24	14.0	0.9	9.5	1
<i>Allium scummetum</i>	Montane moist sun #1	3824	78	43 x 36	24	82	43 x 39	29	9.6	0.21	1.1	1.8
	moist sun #3	4024-36	78	55 x 38	39	59	55 x 39	31	9.0	0.3	1.3	2.2
	moist sun #3	4024-L	60	51 x 35	35	68	51 x 39	31	14.0	0.3	2.1	3.5
	wet sun #1	3824	75	47 x 39	35	68	47 x 35	27	15.0	0.35	2.6	4.3
	dry shade	3284	38	51 x 43	35	48	51 x 39	31	12.0	0.3	1.8	3.0
	Alpine sun	3282	68	47 x 43	31	96	47 x 39	35	7.5	0.2	0.8	1.3
	lath house	3622-26	34	47 x 39	31	38	47 x 39	31	7.2	0.15	0.6	1
	lath house	3622-L	55	43 x 39	27	42	47 x 39	31	14.0	0.2	1.4	2.3
<i>Allium carnum</i>	Montane moist sun #1	3244	39	47 x 39	31	63	48 x 39	27	20.0	0.25	2.5	1.6
	moist sun #3	39424	66	43 x 37	27	50	43 x 31	24	16.0	0.2	1.4	1
	native shade	---	40	51 x 39	31	38	51 x 35	39	0.5	0.2	7.2	4.6
	Alpine sun	3242	62	51 x 35	27	53	51 x 39	27	11.6	0.3	1.7	1.1
<i>Carduus eriophorus</i> ( <i>Cirsium hookerianum</i> )	Montane dry sun	----	24	47 x 24	24	156	31 x 24	14	29.0	5.5	100.3	1.8
	wet sun #2	----	14	39 x 24	20	79	33 x 29	18	43.0	6.6	123.0	2.2
	half shade	----	19	39 x 28	16	89	29 x 23	18	25.0	4.0	58.5	1.1
	full shade	----	11	31 x 24	19	74	31 x 24	20	27.0	6.0	78.7	1.4
	Alpine sun native	----	22	35 x 24	16	168	27 x 24	19	23.0	4.2	66.0	1
<i>Erigeron glabellus</i>	Montane moist sun #1	36C414	99	27 x 22	18	98	27 x 27	18	4.7	1.5	3.0	1
	wet sun #1	36C414	87	31 x 24	16	78	33 x 22	16	13.2	2.9	15.3	5.4
	wet sun #1	36C414	139	27 x 24	14	148	27 x 24	14	5.2	1.8	4.6	1.5
	dry shade	3044	34	31 x 28	16	75	35 x 29	20	14.1	3.1	18.0	6.0
	moist shade	3544	10	33 x 24	20	89	37 x 29	20	12.6	4.8	34.0	11.3
	Alpine sun	3742	63	31 x 27	20	80	39 x 25	16	3.9	2.2	5.4	1.8
<i>Erigeron macranthus</i>	Montane moist sun #1	3844	156	27 x 22	14	156	31 x 24	16	6.3	1.8	7.3	4.9
	wet sun #1	3874	135	27 x 24	14	118	31 x 27	16	7.4	1.8	10.8	6.8
	moist sun #3	3874	158	31 x 27	20	133	31 x 27	20	7.9	2.2	12.7	8.5
	wet sun #1	3874	159	24 x 20	16	82	31 x 27	16	5.8	1.9	7.6	5.1
	moist shade	3874	78	27 x 24	16	76	27 x 25	16	9.7	1.5	11	7.3
	lath house #2	3874	66	27 x 24	16	114	31 x 24	16	8.0	2.4	15.8	8.8
	Alpine sun	3842	241	27 x 24	16	191	27 x 24	16	3.1	0.8	1.8	1.2
	sun	4042	109	31 x 24	16	168	31 x 27	16	3.6	0.7	1.8	1
<i>Oxum turbinatum</i>	Plains wet sun	3525	90	35 x 27	16	65	39 x 27	20	14.3	3.6	23.1	6.6
	Montane moist sun #1	3224	88	31 x 27	16	108	35 x 27	20	6.1	2.0	6.2	1.8

Table 47 (Cont.). Frequency and dimensions of stomata of transplants in the adaptation gardens in Colorado. The outside dimensions of the guard cells and length of stomatal opening (LSO) are both in microns.

Species	Habitat	Stake label	Upper epidermis		Lower epidermis		Leaf dimensions			Relative leaf area			
			Stoma	LSO	Stoma	LSO	Length	Width	Area				
Oenothera biennis	Montane moist sun #3	4024-L	85	31 x 20	16	75	35 x 24	20	8.8	2.1	9.0	2.6	
	moist sun #3	4024-S	68	35 x 24	20	88	39 x 24	20	4.5	1.5	3.5	1.2	
	wet sun #1	3884	119	31 x 24	16	77	35 x 25	18	7.3	1.3	4.1	1.2	
	moist shade	3884	76	39 x 27	20	79	35 x 24	18	12.5	2.0	13.6	3.9	
	lath house#1	3224	102	31 x 24	16	79	35 x 27	20	20.0	3.8	29.8	8.5	
	Alpine sun garden	3222	113	35 x 27	16	90	35 x 27	16	8.8	2.2	7.9	2.3	
	sun (extrinsic)	-----	98	39 x 27	20	76	43 x 27	24	19.5	4.2	45.1	12.9	
	eunibulbata	-----	151	31 x 24	16	98	35 x 24	20	5.5	1.6	4.8	1.4	
	lath house	3622-L	32	43 x 27	22	40	43 x 21	27	11.0	5.2	32.2	9.2	
	lath house	3622-S	63	31 x 24	16	49	35 x 27	16	7.5	2.5	6.2	2.3	
	lath house	3222	70	31 x 22	14	65	31 x 24	16	11.0	2.8	14.0	4.0	
	Summit (14000ft)	-----	85	45 x 24	16	66	39 x 27	24	7.1	2.5	7.9	2.3	
	Mertensia sibirica	Montane moist sun #3	3844	1	24 x 16	10	224	24 x 24	18	9.7	4.3	35.7	4.1
		moist sun #3	4024-S	0	20 x 20	20	823	24 x 20	12	6.7	3.1	14.2	1.7
moist sun #3		4024-L	0	-----	-----	191	25 x 20	12	8.0	3.5	22.1	2.7	
wet sun #1		3844	0	-----	-----	372	24 x 20	8	6.0	1.9	8.3	1	
wet sun #2		-----	0	-----	-----	224	27 x 20	12	10.5	4.4	32.4	3.9	
lath house#1		3144	0	-----	-----	435	20 x 18	8	10.8	7.4	62.5	7.5	
lath house#2		-----	0	-----	-----	185	27 x 16	12	10.4	4.2	33.2	4.0	
Alpine sun garden		3842	32	27 x 18	10	278	27 x 20	10	6.7	3.1	14.5	1.7	
above pool		-----	4	27 x 16	10	262	29 x 16	12	5.5	2.6	10.2	1.2	
below pool		-----	14	23 x 16	10	272	27 x 20	12	8.5	4.2	24.9	3.0	
ravine		-----	7	24 x 16	10	180	27 x 20	12	5.8	4.4	27.1	3.5	
lath house		3142	10	27 x 20	10	129	24 x 16	10	9.2	3.6	26.2	3.2	
Monarda fistulosa		Montane dry sun	-----	53	25 x 24	12	326	24 x 20	16	3.0	1.3	2.6	1
		moist sun #1	-----	49	27 x 27	16	293	24 x 20	12	6.4	2.5	10.4	4.0
	moist sun #3	40424	32	27 x 24	12	244	27 x 24	14	7.0	2.7	10.9	4.2	
	lath house#1	-----	0	-----	-----	139	24 x 20	12	8.4	4.4	24.1	9.3	
	Alpine sun	4042	39	27 x 24	16	198	31 x 27	16	8.5	1.6	5.6	1.4	
	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
Folemonium confertum	Montane moist sun #1	3224	26	39 x 31	24	45	43 x 31	20	0.5	0.25	---	---	
	dry shade	-----	24	35 x 27	16	32	39 x 27	24	0.4	0.2	---	---	
Folemonium speciosum	Alpine native	-----	37	39 x 31	24	67	43 x 31	27	0.8	0.6	---	---	
Potentilla nivea	Montane moist sun #3	3824	40	35 x 25	22	143	31 x 24	20	3.8	5.5	10.5	2.4	
	lath house#3	3824	20	33 x 24	18	96	31 x 24	18	6.0	8.3	24.0	5.6	
	moist shade	3824	66	35 x 27	24	151	35 x 25	20	2.8	3.8	5.4	1.3	
	Alpine native sun	-----	95	31 x 27	20	149	33 x 27	20	2.2	2.5	4.3	1	
Sedum roseum	Montane moist sun #2	3724	92	35 x 24	20	55	35 x 27	20	1.1	0.5	---	---	
	wet sun #1	3724	88	35 x 27	16	56	35 x 27	22	1.6	0.8	---	---	
	dry shade	-----	40	39 x 31	20	17	39 x 24	24	1.7	0.9	---	---	
	moist shade	2724	52	31 x 20	16	83	29 x 20	16	1.0	0.6	---	---	
	Alpine sun native	-----	65	39 x 20	20	43	43 x 24	24	2.4	0.9	---	---	
	Summit (14000 ft)	-----	72	35 x 27	20	66	31 x 24	16	1.2	0.7	---	---	
Sedum stenopetalum	Montane moist shade	-----	17	39 x 27	24	-----	-----	-----	1.5	0.3	---	---	
	dry shade	-----	20	31 x 24	16	-----	-----	-----	1.0	0.25	---	---	
	dry sun (normal)	-----	19	27 x 24	16	-----	-----	-----	0.6	0.2	---	---	
	dry sun (extrinsic)	-----	78	27 x 24	14	-----	-----	-----	0.8	0.2	---	---	
	Alpine sun native	-----	40	31 x 29	18	-----	-----	-----	1.0	0.25	---	---	
	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
Solidago nana	Flaine sun	3525	109	35 x 24	20	66	31 x 27	18	8.6	2.3	9.6	7.9	
	Montane moist sun #3	3884	67	33 x 29	20	50	35 x 31	20	11.7	2.3	18.0	10.0	
	moist sun #3	4024-S	99	39 x 29	24	87	35 x 31	20	6.2	1.6	5.4	4.5	
	moist sun #3	4024-L	119	33 x 27	18	95	35 x 29	18	6.3	1.9	5.9	4.9	
	wet sun #1	3884	73	35 x 27	20	59	39 x 31	24	6.2	1.8	6.2	5.8	
	moist shade	3884	60	35 x 24	20	50	35 x 27	20	11.4	2.0	9.6	8.0	
	lath house#2	3324	59	31 x 27	20	59	33 x 27	18	8.3	1.8	7.1	5.9	
	Alpine sun native	-----	106	31 x 27	16	85	33 x 27	16	2.8	1.8	3.2	2.7	
	lath house	3222	66	31 x 22	18	69	43 x 31	16	1.3	0.9	1.8	1	
	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
Solidago nemoralis	Flaine sun	3158	225	29 x 22	18	168	27 x 24	14	13.0	2.7	20.0	6.2	
	lath house	3655	87	43 x 27	24	70	47 x 31	24	19.0	2.5	30.7	9.6	
	Montane moist sun #3	3644	166	27 x 23	12	119	31 x 24	12	14.0	2.9	19.3	6.0	
	moist sun #1	3164	175	25 x 23	16	113	27 x 24	14	12.7	2.9	21.3	6.7	
	wet sun #1	36554	185	27 x 24	12	168	29 x 22	18	18.0	2.3	14.7	4.6	
	lath house#1	3644	86	27 x 22	14	78	31 x 24	14	14.1	2.3	9.5	3.0	
	lath house#2	3354	86	31 x 24	14	75	31 x 24	16	13.0	2.6	18.1	5.7	
	Alpine sun	4042	88	35 x 24	16	89	35 x 20	18	5.8	1.1	3.2	1	
	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
Thalictrum fendleri	Flaine sun	3045	-----	-----	-----	334	27 x 20	8	1.4	1.8	1.3	1	
	lath house	36455	-----	-----	-----	181	27 x 20	10	2.6	2.3	4.5	3.5	
	Alpine sun	3142	-----	-----	-----	270	27 x 24	12	1.5	1.7	1.7	1.3	

Note: Length and width of leaves are in centimeters, while the leaf areas are in square centimeters. Relative leaf areas apply only within a species. When no stomata are given none are present except for *Sedum stenopetalum* which was considered as a round leaf.



## GLOSSARY

- Acclimatization**—A process of adaptation by which animals and plants are gradually rendered capable of surviving and flourishing under meteorological conditions different from those to which they have been accustomed.
- Allogamy**—Cross-fertilization.
- Alpine**—Above timberline.
- Anemometer**—An instrument for measuring the velocity of the wind.
- Antho-carpotropic**—Pertaining to movements of flower and fruit.
- Anthokinetics**—The opening and closing rhythm of flowers.
- Atmometer**—An instrument for measuring the amount of evaporation from a humid surface.
- Autogamy**—Self-fertilization.
- Bunchgrass**—Term applied to a grass that forms a distinct clump.
- Chresard**—The available water of the soil; the physiological water-content.
- Climax**—The final stage in the development of vegetation which continues to occupy an area as long as the climate remains unchanged. The *alpine climax* for instance is the vegetation typical of the climate above timberline, and the *montane climax*, the forests of spruce and fir characteristic of mountain regions at altitudes between the plains and timberline.
- Clisere**—The series of climax formations or zones which follow each other in a particular climatic region, in consequence of a distinct change of climate.
- Clone**—The transplanted portion of the same seedling individual.
- Constancy**—The range of variation within the group of individuals.
- Convergence**—A close similarity of structure between two distinct though allied genera or species.
- Conversion**—The morphological similarity between two distinct though allied species or genera so close that neither can be distinguished from the other.
- Diastrophic**—Pertaining to upheavals or displacements of the earth's crust.
- Disclimax**—A modification or replacement of the true climax, either as a whole or in part, chiefly as a consequence of disturbance by

man or domesticated animals, such as fire, lumbering, or over-grazing, etc.

**Dominant**—An organism so well adjusted to a given set of conditions that it becomes controlling wherever these conditions occur; the chief constituent of a plant community.

**Ecad**—A habitat form due to adaptation to the environment.

**Ece**—The habitat.

**Ecesis**—The phenomenon exhibited by an invading disseminule from the time it enters a new community until it becomes thoroughly established.

**Ecial**—Pertaining to the habitat.

**Ecogenesis**—The origin of new forms under the influence of the environment.

**Ecogenic**—Originating through adaptation to the habitat.

**Ecology**—The science of the relationship of organisms to the environment.

**Ecotone**—The line along which two types of vegetation compete for the same ground.

**Ecotype**—An ecad which responds slowly, if at all, to a change of environment.

**Edaphic**—Influenced or produced by the soil or its contents.

**Faciation**—A concrete subdivision of the association, the entire area of the latter being made up of its various faciations, except for successional stages or fragments of the several consociations. Each faciation corresponds to a particular regional climate of real but smaller differences in rainfall/evaporation and temperature.

**Fixation**—The accumulation of a new habit or response until it becomes hereditary.

**Fixity**—Stability.

**Forb**—An herbaceous plant which is not a grass.

**Gametic**—Pertaining to gametes or germ-cells.

**Geophyte**—A plant which produces underground buds that do not develop there.

**Habitat**—The place in which a plant grows.

**Holarctica**—The entire arctic region.

**Holard**—The total water-content of the soil.

**Hybrid**—A form arising from cross-fertilization between two different varieties, species or genera.

**Hybrid-mutant**—A mutant arising through hybridization.

- Hydroid**—Living in the water.
- Hydrophyte**—A plant which grows in water; an aquatic plant.
- Hydrophytic**—Conditions favorable to hydrophytes.
- Hygrothermograph**—An instrument for indicating and recording simultaneous values of temperature and relative humidity.
- Hypertrophy**—Overgrowth through excessive nutrition.
- Hypotrophy**—An abnormal state due to defective nutrition.
- Linneon**—A Linnean species.
- Lociation**—A local variant of an association, varying in composition of the important subdominants and influents, as distinguished from faciation, the local variant based on the presence of dominants.
- Louvered**—Closed with broad slats sloping downward and outward and with openings between.
- Meiosis**—Same as mitosis: nuclear division.
- Meitotic**—Characterized by mitosis, i.e. the splitting of the chromatin of a nucleus.
- Meristem**—Undifferentiated, actively dividing cells.
- Mesocline**—A moist, cool slope.
- Mesophyll**—The soft inner tissue of leaves.
- Mesophytic**—Medium moisture.
- Midalpine**—Altitudes above 12,000 feet.
- Midgrass**—A grass of medium height between shortgrass and tallgrass. i.e. *Agropyrum*, *Elymus*, etc.
- Migrule**—The unit or agent of migration.
- Mitosis**—The splitting of the chromatin of a nucleus.
- Mitotic**—Having to do with mitosis.
- Montane**—The middle altitude on a mountain slope.
- Morphogenic**—Morphological with special reference to origin.
- Morphogeny**—The science of the forms of living bodies with respect to their genesis or evolution.
- Morphology**—The science of the outer form and internal structure, without regard to the functions, of plants and animals.
- Mutant**—An individual that differs from the type form, arising by discontinuous variation.
- Osmotic**—Concerning the pressure which causes diffusion between solutions of differing concentration.
- Pelory**—A monstrosity.

**Phenological**—Concerning the dates of budding, leafing, blooming and fruiting of plants in connection with meteorological conditions.

**Photometer**—An instrument to measure the intensity of light.

**Stop-watch Photometer**—A simple type of photometer by means of which intervals of exposure of sensitive paper to the light is controlled by a stop-watch.

**Phylad**—A continuous series of related species, of which one is ancestral and the others derived.

**Phylogenetic**—Pertaining to phylogeny as distinguished from ontogeny.

**Phylogeny**—That branch of biology which treats of the ancestral history of animals or plants.

**Phytometer**—A plant measure designed to express the physical factors of the habitat in terms of physiological activities. It consists of plants grown, at least for a time, in the several habitats that are to be compared. Several plants are used in each habitat so that variability of the individual is checked out.

**Phytometric**—Measured by phytometers.

**Polydemic**—Growing in several countries.

**Proclimax**—A more or less permanent community resembling the climax in one or more respects, but gradually replaceable by the latter when the control of climate is not inhibited by disturbance. Includes subclimax, disclimax, preclimax and postclimax.

**Pyranometer**—An instrument for the measurement of direct solar and sky radiation.

**Pyrheliometer**—An instrument for measuring the heat of the sun.

**Quadrat**—A square area of varying size marked off for purposes of detailed study of the vegetation, such as the relative abundance and importance of each species.

**Radio-atmometer**—A pair of spherical atmometers — one black, one white.

**Reversibility**—The causes or processes by which a character may be lost or regained.

**Segregate**—A member of a group dissociated from the rest.

**Seral**—Developmental; not static.

**Sere**—A unit succession, comprising the development of a formation from the pioneer stage through successional stages to the final climax.

- Somatic**—Concerned with vegetative rather than reproductive processes.
- Specient**—An individual of a species.
- Subalpine**—The elevation next below the alpine.
- Subclimax**—The stage in both primary and secondary seres that immediately precedes the climax. An imperfect stage of development, in which the vegetation is held indefinitely either by natural or artificial factors other than climate, such as grazing, burning, cutting, etc.
- Subdominant**—A species of lower life-form than that of the dominants of a climax, but which may appear more abundant or conspicuous than the latter at certain seasons of the year. For example, trees and shrubs are more conspicuous in a savanna than the grasses, although the latter are in actual control of the habitat. Similarly, the dominant grasses of the prairie may be more or less concealed during the growing season, by tall forbs.
- Terad**—A pelory or monstrosity; malformation.
- Teratogenesis**—The production of monsters, or malformations.
- Teratogeny**—The treatment of malformation, or monstrous or abnormal growths.
- Teratology**—Same as teratogeny.
- Thermograph**—An automatic self-registering thermometer.
- Transect**—A continuous narrow strip that gives a cross section of vegetation. It may be either a line or a belt of certain width.
- Traumatic**—Of or pertaining to wounds.
- Tundra**—A level treeless area with an arctic climate.
- Variad**—A form differing from the typical species, in secondary modifications.
- Variant**—Same as variad.
- Voucher**—A plant specimen which serves to confirm or establish facts.
- Xerad**—A xerophyte.
- Xeric**—Pertaining to dry habitats.
- Xerocline**—A dry, warm slope.
- Xeroid**—Same as xeric.
- Xerophyte**—A plant adapted to living under conditions of small available moisture.
- Xerophytic**—Having the character or some feature of a xerophyte; dry, or lacking available moisture.
- Xerophytism**—Adaptation to arid conditions.



## SUPPLEMENTAL REFERENCES

Practical considerations have made it necessary to omit the original comprehensive bibliography and to list here only such publications as are either mentioned in the text, or that have appeared in connection with the main research during the period covered by it. The latter have adequate bibliographies in their respective subjects and are, for the most part, still available for reference.

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## SPECIES FROM EUROPE

### SPECIES FROM FOREIGN BOTANIC GARDENS FOR USE IN THE EXPERIMENTAL GARDENS IN CALIFORNIA AND COLORADO.

#### DENMARK

<i>Acanthospermum humilum</i>	<i>Geum rivale</i> x <i>urbanum</i>
<i>Achillea t.rosea</i>	<i>Globularia vulgaris</i>
<i>Achyrachaena mollis</i>	<i>Helianthella quinquenervis</i>
<i>Alisma plantago</i>	<i>Humen elegans</i>
<i>Anemone multifida</i>	<i>Jasione montana</i>
<i>nemorosa</i>	<i>Jaegeria hirta</i>
<i>ranunculoides</i>	<i>Koeleria phleoides</i>
<i>Antheophora elegans</i>	<i>Knautia arvensis</i>
<i>Arctium lappa</i>	<i>Lasiospermum radiatum</i>
<i>minus</i>	<i>Lepidium perfoliatum</i>
<i>Armeria alpina</i>	<i>Lepturus filiformis</i>
<i>vulgaris</i>	<i>Leucopsis diffusa</i>
<i>v.maritima</i>	<i>Melitella pusilla</i>
<i>Asarum canadense</i>	<i>Micropus erectus</i>
<i>europaeum</i>	<i>Morina longifolia</i>
<i>Aster alpinus</i>	<i>Moscharia pinnatifida</i>
<i>novi-belgii</i>	<i>Myosurus minimus</i>
<i>Avena elatior</i>	<i>Myriactis nepalensis</i>
<i>Batrachium acceleratum</i>	<i>Odontospermum acquaticum</i>
<i>Berkheya radula</i>	<i>Pentstemon arizonicus</i>
<i>Blainvillea rhomboidea</i>	<i>hartwegii</i>
<i>Brizopyrum siculum</i>	<i>tubiflorus</i>
<i>Bupththalmum speciosum</i>	<i>Phleum asperum</i>
<i>Callistemma brachiata</i>	<i>Phyteuma limonifolium</i>
<i>Campanula alliarifolia</i>	<i>Plantago arenaria</i>
<i>Castellia tuberculata</i>	<i>aristata</i>
<i>Cenia turbinata</i>	<i>Psamma arenaria</i>
<i>Cephalaria alpina</i>	<i>Pterotheca nemausensis</i>
<i>syriaca</i>	<i>Pulsatilla alpina</i>
<i>tartarica</i>	<i>Ranunculus auricomus</i>
<i>Chamaenerium latifolium</i>	<i>Relhania sessiliflora</i>
<i>Clematis alpina</i>	<i>Scabiosa columbaria</i>
<i>Coreopsis coronata</i>	<i>Sclerocarpus uniserialis</i>
<i>Crupina vulgaris</i>	<i>Scutellaria laterifolia</i>
<i>Cryptostemma calendulaceum</i>	<i>parvula</i>
<i>Cymboseria palaestina</i>	<i>Senecio alpinus</i>
<i>Delphinium elatum</i>	<i>Sesleria argentea</i>
<i>exaltatum</i>	<i>Solanum nigrum</i>
<i>Diarrhena americana</i>	<i>Solidago arguta</i>
<i>Dichrocephala latifolia</i>	<i>virgaurea</i>
<i>Dinebra arabica</i>	<i>Soliva anthemidifolia</i>
<i>Dipsacus pilosus</i>	<i>Stipa calamagrostis</i>
<i>Echinacea purpurea</i>	<i>capillata</i>
<i>Echinodorus macrophyllus</i>	<i>gigantea</i>
<i>ranunculoides</i>	<i>pennata</i>
<i>Eclipta erecta</i>	<i>vaseyi</i>
<i>Elivira martyni</i>	<i>Syndrella nodiflora</i>
<i>Elymus arenarius</i>	<i>Thalictrum minus</i>
<i>glauca</i>	<i>Tridax trilobata</i>
<i>sibiricus</i>	<i>Triglochin maritimum</i>
<i>Erigeron macranthus</i>	<i>palustre</i>
<i>pulchellus</i>	<i>Triticum monococcum</i>
<i>speciosus</i>	<i>spelta</i>
<i>s.grandiflorus</i>	<i>Tussilago farfarus</i>
<i>s. superbus</i>	<i>Typha gracilis</i>
<i>Ethulia conyzoides</i>	<i>Ursinia anthemoides</i>
<i>Festuca vesiciata</i>	<i>Verbena stricta</i>
<i>Fragaria vesca</i>	<i>Viola tricolor</i>
<i>Gaillardia pulchella</i>	<i>Xanthocephalum gymnospermoides</i>

## ENGLAND

*Androsace chamaejasme*  
*Anemone alpina*  
     *decapetala*  
     *narcissiflora*  
     *nemorosa*  
     *occidentalis*  
     *patens*  
*Aquilegia canadense* *nana*  
     *chrysantha*  
     *formosa*  
     *vulgaris* x *alpina*  
*Brodiaea californica*  
*Campanula alpina*  
*Cypripedium californicum*  
*Delphinium menziesi*  
*Dodecatheon alpinum*  
     *giganteum*  
     *meadia*  
*Draba aurea*  
*Epilobium obcordatum*  
*Erigeron glacialis*  
     *leiomerus*  
     *radicatus*  
     *salsuginosus*  
*Erysimum pumilum*  
*Erythronium californicum*  
     *giganteum*  
*Gaura lindheimeri*  
*Gentiana affinis*  
     *crinita*  
     *parryi*  
*Lewisia nevadensis*  
*Lupinus plattensis*

*Mimulus cardinalis aureus*  
     *guttatus*  
*Papaver alpinum*  
     *nudicaule*  
*Pentstemon angustifolius*  
     *azureus*  
     *barbatus*  
     *confertus*  
     *cristatus*  
     *cyananthus*  
     *fruticosus*  
     *glaber*  
     *glaucus roseus*  
     *hallii*  
     *humilis*  
     *isophyllus*  
     *menziesii*  
     *newberryi*  
     *procerus*  
     *secundiflorus*  
     *torreyi*  
*Polemonium confertum eximium*  
*Polygonum alpinum*  
     *viviparum*  
*Pyrola rotundifolia*  
*Silene acaulis*  
*Sisyrinchium douglasi*  
     *grandiflorum*  
*Solidago alpestris*  
     *virgaurea*  
*Sphaeralcea munroana*  
*Viola canina*  
     *nuttalli*

## FINLAND

*Achillea millefolium rosea*  
     *ptarmica*  
*Agropyrum cristatum*  
*Anemona narcissiflora*  
     *virginiana*  
*Antennaria dioica*  
*Asclepias speciosa*  
*Aster alpinus ruber*  
     a. *superbus*  
*Cerastium alpinum*  
     a. *lanatum*  
*Cerinth alpinum*  
*Clematis alpina sibirica*  
*Elymus arenarius*  
     *giganteus*  
     *sibiricus*  
*Erigeron caccasacusus*  
     *coulteri*  
     *grandiflorus*  
     g. *elatior*  
*Eryngium alpinum*  
*Erythronium dens-canis*  
*Festuca rubra alpina*  
*Geum coccineum*  
     *intermedium*  
     *japonicum*  
*Helianthus rigidus*

*Liatris elegans*  
     *macrostachya*  
*Oxalis valdiviana*  
*Oxyria digyna elatior*  
*Papaver alpinum*  
     *radicatum*  
*Pentstemon alpinus*  
     *glaber alpinus*  
*Phleum alpinum*  
*Potentilla gracilis rigida*  
*Pulsatilla alpina*  
     a. *sulphurea*  
     *rubra*  
*Rumex acetosa*  
     *alpinus*  
     *cordifolius*  
     *fennicus*  
     *gmelini turcz*  
     *hydrolapathum*  
     *mexicanus*  
     *patientia*  
*Sanguisorba alpina*  
*Scandix pecten-veneris*  
*Sidalcea candida*  
     *malviflora*  
     m. *listeri*  
     m. *purpurea*

*Silene alpina*  
*Sisyrinchium bermudianum*  
     *occidentale*  
*Solidago mollis*  
*Specularia speculum-veneris*  
*Trollius europaeus*

*Verberna aubletia*  
     *hastata*  
     *stricta*  
*Veronica alpina*  
*Viola pedatifida*

## FRANCE

*Agropyrum junceum*  
*Alisma plantago*  
*Andropogon ischaemum*  
*Butomus umbellatus*  
*Chaeturus fasciculatus*  
*Damasonium stellatum*  
*Demazeria sicula*  
*Dinebra arabica*  
*Elymus glaucus*  
*Heleochoa alopecuroides*  
*Lygicum spartum*  
*Molinia coerulea*  
*Oxalis acetosella*  
     *cernua*  
     *corniculata*  
     *crenata*  
     *depeii*

*Phleum alpinum*  
*Psilurus nardoides*  
*Rumex conglomeratus*  
     *crispus*  
     *hymenosepalus*  
     *intermedia*  
     *monticola*  
     *patientia*  
     *pulcher*  
*Schismus marginatus*  
*Sesleria argentea*  
*Stipa aristella*  
     *capillata*  
     *pennata*  
*Tropaeolum peregrinum*

## GERMANY

*Achillea millefolium*  
*Aira flexuosa*  
*Agastache anethiodora*  
*Agrimonia eupatoria*  
     *parviflora*  
*Agropyrum elongatum*  
     *sibiricum*  
     *tenerum*  
*Agrostemma githago*  
*Anemone narcissiflora*  
     *virginiana*  
*Antennaria dioica*  
     *d. americana*  
     *imbricata*  
     *neodioica*  
     *plantaginca*  
     *speciosa*  
*Asclepias speciosa*  
*Aster alpinus*  
     *azureus*  
     *drummondii*  
     *laevis*  
     *novi-belgii*  
     *shortii*  
     *turbinellus*  
     *umbellatus*  
*Bromus ciliatus*  
     *inermis*  
*Campanula rotundifolia*  
     *r. olympica*  
*Centaurea alpina*  
*Chelone glabra*  
     *lyoni*  
     *obliqua*  
*Delphinium azureum*  
     *menziesii*  
*Echinacea purpurea*

*Elymus dahuricus*  
     *giganteus*  
     *glaucus*  
     *hirsutiglumis*  
     *sibiricus*  
     *virginicus*  
*Epilobium hornemanii*  
*Erigeron compositus trifidus*  
     *elongatus*  
     *eriocephalus*  
     *glandulosus*  
     *salsuginosus*  
     *subtrinervis*  
*Erinus alpinus*  
*Eryngium alpinum*  
*Festuca alpina*  
     *ovina*  
     *o. supina*  
     *rubra*  
*Helianthus decapetalus*  
     *mollis*  
*Hieracium alpinum*  
*Koeleria albenscens*  
     *glauc*  
*Liatris ligustistylis*  
*Linum alpinum*  
*Luzula campestris congesta*  
     *nivea*  
*Mimulus alpinus*  
*Oenothera fruticosa*  
     *muricata*  
*Oryzopsis juncea*  
*Papaver alpinum*  
     *radicatum*  
*Pentstemon coeruleus*  
     *glaucus stenosepalus*  
     *secundiflorus*



<i>Poa alpina</i>	<i>graminifolia</i>
<i>Potentilla arguta</i>	<i>ohioensis</i>
<i>a. convallaria</i>	<i>ridellii</i>
<i>glandulosa</i>	<i>rigida</i>
<i>gracilis</i>	<i>uliginosa</i>
<i>g. rigida</i>	<i>virgaurea</i>
<i>pennsilvanica</i>	<i>Spartina cynosuroides</i>
<i>pulcherrima</i>	<i>Sporobolus wrighti</i>
<i>Ranunculus acer</i>	<i>Stipa arundinacea</i>
<i>Rudbeckia amplexicaulis</i>	<i>calamagrostis</i>
<i>bicolor</i>	<i>krosakorum</i>
<i>flava</i>	<i>lagascae</i>
<i>laciniata</i>	<i>sibirica</i>
<i>Rumex alpinus</i>	<i>s. effusa</i>
<i>chrysocarpus</i>	<i>tortilis</i>
<i>hydrolapathum</i>	<i>Thelesperma filifolium</i>
<i>hymenosepalus</i>	<i>Thermopsis arenosa</i>
<i>maritimus</i>	<i>Tinantia erecta</i>
<i>patientia</i>	<i>Townsendia grandiflora</i>
<i>Scutellaria alpina lupulina</i>	<i>Tradescantia virginica</i>
<i>lateriflora</i>	<i>Tripsacum dactyloides</i>
<i>tuberosa</i>	<i>Trisetum flavescens</i>
<i>Secale cereale</i>	<i>Triticum caninum</i>
<i>Sidalcea neo-mexicana</i>	<i>rigidum</i>
<i>oregona</i>	<i>setosum</i>
<i>Sieversia montana</i>	<i>versicolor</i>
<i>Silene armeria</i>	<i>Trollius europaeus</i>
<i>Sisyrinchium angustifolium</i>	<i>Troximon auriantiacum</i>
<i>chilense</i>	<i>Verbena canadensis</i>
<i>montanum</i>	<i>hastata</i>
<i>striatum</i>	<i>urticifolia</i>
<i>Solidago alpestris</i>	<i>Viola pedatifida</i>
<i>bicolor</i>	<i>pinnata</i>
<i>elongata</i>	<i>tricolor</i>
<i>glomerata</i>	<i>t. sabulosa</i>

## HOLLAND

<i>Anemone pulsatilla</i>	<i>Echinacea purpurea</i>
<i>p. rubra</i>	<i>Haplopappus coronopifolius</i>
<i>Aquilegia flavescens</i>	<i>Polanisia graveolens</i>
<i>Artemisia dracunculus</i>	<i>Vernonia altissima</i>
<i>Asclepias speciosa</i>	<i>fasciculata</i>

## SWEDEN

<i>Agropyrum caninum</i>	<i>Koeleria alpicola</i>
<i>carinatum</i>	<i>Oenothera purpurea</i>
<i>cristatum</i>	<i>Oxalis adenophylla</i>
<i>marginatum</i>	<i>lactea</i>
<i>tenerum</i>	<i>lasiandra</i>
<i>Aster alpinus</i>	<i>lasiopetala</i>
<i>Bromus breviaristatus</i>	<i>Poa alpina</i>
<i>Carex atrata</i>	<i>Rumex altissimus</i>
<i>capitata</i>	<i>aquaticus</i>
<i>Ehrharta erecta</i>	<i>auriculatus</i>
<i>Elymus arenarius</i>	<i>crispus</i>
<i>canadensis</i>	<i>obtusifolius</i>
<i>sabulosus</i>	<i>occidentalis</i>
<i>Erigeron ramosus</i>	<i>patientia</i>
<i>Eryngium alpinum</i>	<i>salicifolius</i>
<i>Haynaldia villosa</i>	<i>scutatus</i>
<i>Hierochloa odorata</i>	<i>steudelii</i>
	<i>vesicarius</i>

*Sisyrinchium* graminifolium  
 junceum  
 tenuifolium

*Stipa* calamagrostis  
 gigantea  
 longifolia  
 pennata  
 splendens  
*Thalictrum* alpinum

## SWITZERLAND

*Alisma* plantago  
*Alsine* verna  
*Alyssum* alpestre  
*Androsace* chamaejasme  
 glacialis  
*Anemone* alpina  
 caroliniana  
 decapetala  
 narcissiflora  
 nemorosa  
 pulsatilla  
*Antennaria* alpina  
*Apios* tuberosa  
*Aquilegia* alpina  
 arctica  
 brevistyla  
 californica  
 formosa  
 vulgaris  
*Arabis* alpina  
*Arctostaphylos* alpina  
*Arisaema* japonica  
*Armeria* alpina  
 maritima  
*Artemisia* nana  
 rupestris  
*Aster* alpinus  
 himalaicus  
 sericeus  
*Astragalus* alpinus  
*Atragene* alpina  
*Bartsia* alpina  
*Calla* palustris  
*Caltha* alpestris  
 biflora  
 gigas  
 palustris  
 polysepala  
*Camassia* esculenta  
*Campanula* alpina  
 carpatica  
 laponica  
 rotundifolia  
 r. alba  
 soldanellaeflora  
*Cardamine* alpina  
*Centaurea* alpina  
*Cephalaria* alpina  
 tartarica  
*Chelone* barbata  
*Chrysanthemum* alpinum  
 articum  
*Clematis* alpina

*Cornus* florida  
 nuttallii  
*Delphinium* azureum  
 exaltatum  
 glaucum  
*Desmodium* canadense  
*Dianthus* acaulis  
 alpestris  
 alpinus  
 carthusianorum  
 glacialis  
*Dicentra* chrysantha  
 eximia  
*Dodecatheon* alpinum  
*Douglasia* montana  
*Dryas* drummondii  
*Encelia* actoni  
*Epilobium* alpinum  
 anagallifolium  
 angustifolium  
*Erigeron* elatior  
 radicans  
 salsuginosus  
 speciosus  
 s. grandiflorus  
 trifidus  
 uniflorus  
*Erinus* alpinus  
*Eritrichium* nanum  
*Eryngium* alpinum  
 a. grandiflorum  
*Erysimum* pumilum  
*Erythronium* dens canis  
 parviflorum  
 revolutum  
*Gentiana* acaulis  
 alpina  
 amarella  
 calycosa  
 detonsa  
 frigida  
 nivalis  
 parryi  
*Geranium* aconitifolium  
 fremonti  
 maculatum  
 pratense  
 sylvaticum  
*Globularia* nana  
 trychosantha  
 vulgaris  
*Goodenia* repens  
*Helenium* hoopesi

- Helianthella quinquenervis*  
     *uniflora*  
*Helianthus orgyalis*  
*Heracleum giganteum*  
*Hesperocallis undulata*  
*Hibiscus militaris*  
*Hutchinsia alpina*  
*Impatiens noli tangere*  
*Isatis alpina vera*  
*Isopyrum thalictroides*  
*Jasione humilis*  
     *montana*  
     *perennis*  
*Knautia arvensis*  
*Leontopodium alpinum*  
*Linaria alpina*  
*Linum alpinum*  
*Lithospermum angustifolium*  
*Lobelia cardinalis*  
     *fulgens*  
     *syphilitica*  
*Luzula albida*  
     *lutea*  
     *sylvatica*  
*Lychnis alpina*  
*Melilotus indicus*  
*Menyanthes trifoliata*  
*Mertensia ciliata*  
     *echioides*  
     *maritima*  
     *paniculata*  
     *primuloides*  
     *virginica*  
*Mimulus alpinus*  
     *luteus*  
     *ringens*  
*Myosotis alpestris*  
*Nuphar luteum*  
*Nymphaea alba*  
     *coerulea*  
*Oenothera glauca*  
     *serrulata*  
*Oxalis acetosella*  
     *oregana*  
*Papaver alpinum*  
     *nudicaule*  
     *radicatum*  
*Parnassia alpina*  
*Paronychia nivea*  
     *serpyllifolia*  
*Pentstemon alpinus*  
     *arizonicus*  
     *cobaea*  
     *linarifolius*  
     *murrayanus grandiflorus*  
     *pygmaeus*  
     *scouleri*  
     *speciosus*  
*Pericome caudata*  
*Petalostemon oligophyllus*  
     *tenuifolius*  
*Phaca alpina*  
*Phleum alpinum*
- Phlomis alpina*  
*Pinguicula alpina*  
*Plantago argenta*  
     *crassifolia*  
     *cynops*  
     *rubrifolia*  
*Podophyllum peltatum*  
*Polanisia graveolens*  
*Polemonium himalaicum*  
     *mellitum*  
*Polygonum alpinum*  
     *viviparum*  
*Potentilla alpestris*  
     *alpina nana*  
     *nivea*  
*Primula acaulis*  
     *farinosa*  
     *parryi*  
*Ranunculus alpestris*  
     *glacialis*  
     *nivicola*  
*Rhodiola integrifolia*  
*Rosa alpina*  
*Rumex alpinus*  
*Salix herbacea*  
*Sarcodes sanguinea*  
*Scrophularia nodosa*  
*Scutellaria alpina*  
     *galericulata*  
*Silene acaulis*  
     *alpestris*  
     *alpina*  
*Sisyrinchium anceps*  
     *californicum*  
     *grandiflorum*  
     *idahoensis*  
     *mucronatum*  
     *strictum*  
*Soldanella alpina*  
*Solidago alpestris*  
     *arctica*  
     *graminifolia*  
     *humilis*  
     *pygmaea*  
     *rigida*  
     *shorti*  
     *spectabilis*  
     *virgaurea*  
*Thalictrum alpinum*  
     *fendleri*  
     *petaloideum*  
*Trifolium alpinum*  
*Trollius asiaticus*  
     *europaeus superbus*  
*Viola latifolia*  
*Veronica alpina*  
     *serpyllifolia*  
*Viola biflora*  
     *canadensis*  
     *lanceolata*  
     *palmata*  
     *pubescens*

## INDEX

References to illustrations are by plate-number in Bold Face.

- Abronia latifolia*, 97, 99  
*Abutilon theophrasti*, 72  
*Acer*, 95  
     *negundo*, 93  
*Achillea*, 21  
     *alpina*, 72, 82, 87, 94, 99  
     *millefolium* **68**, 82, 202  
     *m.alpina*, **8**  
*Aconitum columbianum*, **49**, 172  
*Actinella*, 236  
     *acaulis*, 236  
     *lanata*, 236  
*Adenostoma sparsifolium*, 72, 82, 94  
*Agastache anethiodora*, 81  
     *nepetoides*, 81  
*Ageris*, 235  
     *aurantiaca*, 230  
     *heterophylla*, **14**, 87, 127  
*Agrimonia eupatoria*, 93  
     *striata*, 72, 82  
*Agropyrum*, 132, 241, 243, 246, 247, 258  
     *caninum*, **Figs. 1, 2**, 80, 99,  
         243, 246, 262-265  
     *dasystachyum*, 75  
     *elongatum*, 99  
     *inermis*, 246  
     *pauciflorum*, 246  
     *repens*, 246  
     *scribneri*, **85**, 201, 243, 246  
     *semicostatum*, 99  
     *smithi*, 246, 247  
     *spicatum*, 96, 246  
*Agrostemma githago*, 87, 88, 89, 112, 113  
*Agrostis hiemalis*, 75  
     *verticillata*, 82  
*Aira (Deschampsia) caespitosa*, 243  
*Allium stellatum*, 81, 99  
*Alyssum alyssoides*, 72  
     *maritimum*, 82  
*Amorpha fruticosa*, 79, 93, 99  
*Anagallis arvensis*, 72  
     *linifolia*, 87, 96, 99  
*Anaphalis margaritacea*, 72, 82  
*Anchusa italica*, 75  
*Andropogon furcatus*, 81  
     *glomeratus*, 72, 82  
     *gryllus*, 96, 98  
     *halli*, 81  
     *ischaemum*, 80  
     *saccharoides*, 97, 98  
     *scoparius*, 75  
     *ternarius*, 81  
     *virginicus*, 72, 82  
*Androsace chamaejasme*, 211  
*Anemone canadensis*, 75, 94, 99  
     *caroliniana*, 94, 95  
     *multifida*, 75  
     *patens*, 72, 82, 94  
*Angelica grayi*, **53**, 173  
*Anisacanthus thurberi*, 94, 96  
*Antirrhinum hispanicum*, **12, 17, 21**, 31,  
     32, 34, 72, 82, 87, 88,  
     89, 96, 98, 99, 108, 109,  
     112, 113, 118  
     *majus*, 72  
     *speciosum*, 82  
*Apios tuberosa*, 94  
*Aquilegia*, 213, 214, 215  
     *alpina*, 75  
     *canadensis*, **50**, 79, 93, 172  
     *chrysantha*, 75  
     *coerulea*, 75  
     *sibirica*, 75  
     *truncata*, 87  
*Arctostaphylos bicolor*, 94  
     *manzanita*, 94  
     *pringlei*, 94  
     *pungens*, 94  
*Arctotis grandis*, **29**, 32, 82, 98, 112, 128  
*Argemone hispida*, 80  
*Arhenatherum elatius*, 80, 99  
*Arisaema triphyllum*, 79, 94  
*Aristida purpurea*, 72, 96, 98, 99  
*Ameria alpina*, 82, 94  
     *maritima*, 72, 82  
*Artemisia gnaphalodes*, 236  
     *ludoviciana*, 236  
     *pattersoni*, **79**, 73, 202, 236  
     *scopulorum*, **79**, 202, 236  
     *vulgaris*, 236  
     *v.gnaphalodes*, 211  
*Asarum canadense*, 79, 94  
*Asclepias galioides*, 82  
     *incarnata*, 81  
     *tuberosa*, 94  
     *verticillata*, 73  
*Aster azureus*, 75  
     *canescens*, 72, 82, 96, 99  
     *cordifolius*, 75, 81, 93, 99  
     *ericoides*, 72  
     *levis*, 75  
     *macrophyllus*, 81  
     *multiflorus*, 81  
     *novae-angliae*, 81, 94, 99  
     *novi-belgi*, 75  
     *puniceus*, 94  
     *spinosus*, 82, 99  
     *turbinellus*, 72, 82

- Astragalus crassicaupus*, 94  
*Atamosco atamosco*, 99  
*Atriplex canescens*, 72  
*Avena fatua*, 72, 82  
*Baeria gracilis*, 127  
*Baileya multiradiata*, 82, 99  
*Baptisia australis*, 94  
     *leucophaea*, **73**, 79  
     *multiradiata*, 82, 99  
     *tinctoria*, 79, 94  
*Besseyia plantaginea*, **71**  
*Bignonia cherere*, 82  
     *stans*, 82, 94  
     *venusta*, 82  
*Bistorta* (*Polygonum bistorta*), **55**, 196  
*Bloomeria aurea*, 99  
*Bouteloua*, 75  
     *chondrosioides*, 72  
     *curtipendula*, 72, 82  
     *eriopoda*, 80  
     *filiformis*, 72  
     *gracilis*, 80, 241  
     *hirsuta*, 80  
     *rigidiseta*, 72  
     *trifida*, 72  
     *uniflora*, 241  
*Brassica oleracea*, 73  
*Bromus catharticus* **Fig. 3**, 82, 266  
     *communitatus*, 73, 82  
     *purgans*, **85**  
*Buchloe dactyloides*, 75, 99  
*Bursa*, 216  
*Calamagrostis purpurascens*, 241  
*Calamovilfa gigantea*, 81  
*Calendula officinalis*, 72  
*Callirhoe involucrata*, 72, 82, 87, 96, 99  
*Caltha*, 95  
     *palustris*, 79  
*Calycanthus occidentalis*, 94  
*Campanula alpina*, 75, 94  
     *medium*, 128, 223  
     *olympica*, 72  
     *pyramidalis*, 72  
     *rapunculoides*, 72, 82  
     *rapunculus*, 72  
     *rotundifolia*, **52**, **67**, 75, 94,  
         172, 196, 201, 202  
     *r.alpina*, **66**, **67**  
     *uniflora*, 173  
*Carduus eriocephalus*, **69**, 202  
*Carex*, 95  
     *festiva*, 94  
*Carpenteria californica*, 94  
*Carpinus*, 95  
     *caroliniana*, 93  
*Cassia fasciculata*, 81  
*Castilleja miniata*, 173, 225  
     *occidentalis*, 199  
     *parviflora*, 173, 225  
*Catananche coerulea*, 72  
*Caulophyllum thalictroides*, 94  
*Ceanothus cuneatus*, 94  
     *cyaneus*, 94  
     *incanus*, 94  
     *integerrimus*, 94  
     *megacarpus*, 94  
     *thyrsiflorus*, 94  
*Cercis canadensis*, 79, 93  
     *occidentalis*, 94  
*Chamaedaphne calyculata*, 79, 93  
*Cheiranthus cheiri*, 72  
*Chelone glabra*, 94  
*Chenopodium murale*, 72  
*Chilopsis linearis*, 94  
*Chimaphila maculata*, 94  
     *umbellata*, 94  
*Chloris ciliata*, 99  
*Chrysanthemum coronarium* **11**, **28**, **29**,  
     **32**, **33**, 72, 82, 87, 88, 89, 96, 99,  
     108, 109, 112, 113, 116, 119  
*Cichorieae*, 230, 235  
*Cimifuga americana*, 93  
*Clarkia*, 42  
     *elegans*, **5**, **74**, 87, 88, 99, 120, 226  
     *pulchella*, **23**  
     *rhomboidea*, 88, 89  
*Claytonia virginica*, 79  
*Clematis alpina*, **49**, 172  
*Cleome lutea*, 81  
     *serrulata*, 81  
*Clintonia umbellata*, 79  
*Collinsia bicolor*, 87, 88, 99  
*Commelina coelestis*, 82  
*Convolvulus arvensis*, 72  
     *tricolor*, 72  
*Cooperia drummondii*, 99  
*Coreopsis lanceolata*, 94, 96, 99  
     *l.grandiflora*, **13**, 72, 82, 121  
     *tinctoria*, 72, 82  
*Cornus florida*, 93  
*Corydalis aurea*, **52**, 172  
*Cosmos bipinnatus*, 72, 87, 88, 89  
     *sulphureus*, 72, 87  
*Cowania stansburiana*, 75  
*Crepis*, 216  
     *alpina*, **7**  
*Cynoglossum amabile*, 87, 88  
     *pictum*, 72, 98  
*Cypripedium acaule*, 79, 94  
     *reginae*, 79, 94  
*Dahlia*, 236  
*Dalea formosa*, 72, 82  
*Dasyliroon wheeleri*, 97  
*Datura*, 216  
     *meteloides*, **36**, 82  
     *stramonium*, 81  
     *tatula*, 223  
*Delphinium azureum*, 75  
     *bicolor*, 72, 82  
     *decorum*, 72  
     *elatum*, 72, 82  
     *scopulorum*, **49**, 75, 172

- Dianthus alpinus*, 72  
*barbatus*, 72  
*carthusianorum*, 72, 94
- Dicentra cucullaria*, 94  
*eximia*, 72, 93
- Digitalis gloxinoides*, **1**, **22**, **72**
- Disporum lanuginosum*, 79
- Dodecatheon meadia*, **71**, 79, 94
- Dracocephalum virginianum*, 81
- Drosophila*, 216
- Elymus*, 241, 243, 246, 258  
*ambiguus*, **Fig. 4**, 243, 247, 266-268  
*canadensis*, **84**, 243, 247  
*condensatus*, 96, 97  
*glaucus*, 99  
*virginicus*, 99
- Encelia*  
*actoni*, 82  
*californica*, **28**, 82, 97  
*farinosa*, 82, 97  
*frutescens*, 82  
*media*, 82
- Epigaea repens*, 79, 94
- Epilobium angustifolium*, 193, 196, 225  
*latifolium*, 193
- Eragrostis*, 98, 243  
*biflora*, 73  
*curvula*, 82, 99  
*intermedia*, 82  
*lugens*, 82, 98  
*trichodes*, **Fig. 5**, 269
- Erigeron*, 236  
*canadensis*, 72, 82  
*glabellus*, **58**, **59**, 191, 211, 236, 258  
*glaucus*, 82  
*macranthus*, **58**, **59**, **78**, 73, 82, 84, 91, 211, 236, 258  
*ramosus*, 72, 82, 98  
*salsuginosus*, 236  
*speciosus*, 72, 94, 96  
*uniflorus*, **65**, 75, 201, 202, 236
- Erysimum asperum*, **51**, 72, 172
- Erythronium albidum*, 91  
*americanum*, 79, 91
- Eschscholtzia californica*, **19**, **20**, 82, 97
- Eucalyptus*, 86
- Eupatorium coelestinum*, 81  
*purpureum*, 81
- Euphorbia corollata*, 75, 94
- Fallugia paradoxa*, 72, 94
- Festuca*, 95, 243, 255, 258  
*brachyphylla*, **64**, 94, 201, 246  
*elatior*, 75  
*occidentalis*, 246  
*ovina*, **Fig. 6**, 75, 246, 270, 271  
*rubra*, 75, 246  
*scabrella*, 246  
*thurberi*, 246  
*viridula*, 246
- Fouquieria splendens*, 97
- Franseria bipinnatifida*, **18**
- Frasera speciosa*, **74**, 225
- Fraxinus americana*, 93
- Gaillardia*, 97, 230, 235, 236  
*aristata*, **37**, **78**, 72  
*hybrida*, **37**, **78**, 72, 82, 96, 99, 112
- Galium boreale*, **47**, **62**, 172
- Gaura lindheimeri*, 72, 75, 82, 99
- Gentiana*, 196, 215  
*amarella*, 196  
*frigida*, **8**, **63**, 75, 199, 202
- Geranium*, 215  
*caespitosum*, 196, 215, 258  
*fremonti*, 73  
*maculatum*, 75  
*pratense*, 82  
*richardsoni*, 196, 215, 258
- Geum atrosanguineum*, 73, 87  
*canadense*, 72, 93, 95  
*rivale*, 73, 82  
*strictum*, 72, 82, 87, 96, 99  
*turbatum*, **55**, 94, 156, 173  
*urbanum*, 72, 82
- Gilia capitata*, 89  
*dianthoides*, 127  
*tricolor*, 87, 89, 127
- Godetia*, **11**, 45, 215  
*amoena*, 87, 128, 215  
*dudleyana*, 87  
*fremonti*, 82  
*grandiflora*, 87, 88, 121, 215  
*quadrivulnera*, 97
- Grindelia blakei*, 82, 89  
*squarrosa*, 72
- Gymnolomia multiflora*, 75
- Habenaria psycodes*, 80, 94
- Halesia*, 95  
*carolina*, 79, 93
- Hamamelis*, 95  
*virginiana*, 93
- Haplopappus*, 236  
*ciliatus*, 81
- Helenium autumnale*, 81
- Helianthella parryi*, **80**  
*quinquenervis*, **80**, 81, 238
- Helianthiae*, 235
- Helianthus*, 236  
*annuus*, **9**, **10**, **75**, 27, 35, 37, 72, 82, 106, 107, 112, 115, 116, 141, 142, 143, 154, 156, 157, 158, 159, 162, 163, 226  
*giganteus*, 81  
*maximiliani*, 75  
*mollis*, 81  
*orgyalis*, 81  
*rigidus*, 81, 99
- Heliopsis helianthoides*, 80
- Heliotropium peruvianum*, 72
- Hepatica acutiloba*, 94  
*triloba*, 94
- Hibiscus moschatus*, 93  
*trionum*, 81

- Hilaria jamesi*, 79  
*Houstonia purpurea*, 94  
*Hypochoeris radicata*, 72, 82  
*Hypoxis hirsuta*, 79, 94  
*Iris missouriensis*, 79  
     *pumila*, 72, 82  
     *versicolor*, 79, 94  
*Isomeris arborea*, 82  
*Kalmia latifolia*, 79, 93  
*Koeleria cristata*, 75, 97, 241  
*Lactuca virosa*, 72  
*Lamarckia*, 98  
     *aurea*, 98  
*Lavandula spica*, 72, 82  
*Lepachys columnaris*, 82, 94, 98, 230  
     *pinnata*, 81  
*Leptochloa uninervia*, 99  
*Leptospermum rigidum*, 98  
*Lesquerella argentea*, 72, 99  
*Leucothoe*, 95  
     *catesbaei*, 79, 83  
*Liatris scariosa*, 81  
     *spicata*, 81, 94  
     *squarrosa*, 75  
*Lilium canadense*, 80  
*Linaria bipartita*, 72, 82  
     *canadensis*, 72  
     *maroccana*, 97, 99  
     *vulgaris*, **48**, 72, 82, 98, 99, 172  
*Linum austriacum*, 72  
     *lewisi*, 87, 88, 96  
     *perenne*, 75  
*Lithospermum linearifolium*, 79, 94  
*Lobelia cardinalis*, 81, 94  
*Lonicera sempervirens*, 82  
*Lotus scoparius*, **18**  
*Lupinus*, 233  
     *albifrons*, 99  
     *chamissonis*, **9**  
*Luzula intermedia*, 201  
     *parviflora*, 201  
     *spicata*, **64**, 201  
*Madia elegans*, **15**, **21**, 87, 88, 89,  
     122, 236  
*Malvastrum munroanum*, 72, 80, 99  
*Manisuris cylindrica*, 75  
*Matthiola incana*, **24**, **27**, 72, 82, 89, 128  
*Medicago sativa*, 72, 82  
*Melia*, 220  
*Melica*, 243  
*Melilotus alba*, 72, 96, 99  
*Mentha piperita*, 99  
*Mentzelia*, 214  
     *aurea*, 41, 42  
     *lindleyi*, 128  
     *multiflora*, 214  
     *nuda*, 214  
*Mertensia*, **Frontispiece**, 95, 234, 259  
     *alpina*, 72, 189, 258  
     *lanceolata*, **56**, 189, 258  
     *paniculata*, **57**, 189  
     *pratensis*, **56**, 189, 258  
     *sibirica*, **54**, **57**, 156, 158, 159,  
         173, 258  
     *virginica*, 79, 189  
*Mimulus aurantiacus*, 82  
     *cardinalis*, **17**, 31, 32, 34, 35,  
         87, 108, 109, 112, 113,  
         114, 116, 123  
*Mirabilis multiflora*, 75  
*Monarda fistulosa*, 81  
     *pectinata*, 81  
     *punctata*, 81  
*Muhlenbergia emersleyi*, 72, 75, 82  
     *montana*, 75  
     *torreyi*, 80  
*Myosotis silvatica*, 72  
*Nemophila aurita*, 41  
*Nolina*, 97  
*Oenothera*, 214, 215, 216  
     *biennis*, 72, 82, 99, 224  
     *b.lanceolata*, 82, 97, 99  
     *caespitosa*, **50**, 172  
     *drummondii*, 75, 97  
     *hookeri*, **36**, 72, 82, 97, 99  
     *lamarckiana*, 72, 82, 99  
     *lanceolata*, 72  
     *missouriensis*, 75  
     *rhombipetala*, 72, 82, 99  
     *speciosa*, 215  
     *spiralis*, **18**  
     *tricalyx*, **17**, **35**, 31, 34, 88,  
         97, 112, 117, 121  
*Oenotheraceae*, 213  
*Onagra*, 215  
*Oreocarya virgata*, **51**, 172  
*Oryzopsis miliacea*, 82, 97, 98  
*Ostrya virginiana*, 93  
*Oxalis howei*, 82  
     *cernua*, 97  
     *corniculata*, 72, 82  
     *violacea*, 94, 99  
*Oxydendron arboreum*, 93  
*Oxyria digyna*, 202  
*Panicum*, 255  
     *scribnerianum*, 73, 82  
     *virgatum*, 96  
*Papaver cordifolius*, 94  
     *isophyllus*, 94  
     *nudicaule*, 72  
     *rhoeus*, **26**  
*Paronychia jamesi*, 213  
     *pulvinata*, 213  
*Paspalum leve*, 73  
     *dilatatum*, 82  
     *stramineum*, 75  
*Pentstemon*, 214, 215  
     *albidus*, 75  
     *angustifolius*, 80  
     *antirrhinoides*, 82, 94  
     *arizonicus*, 72  
     *barbatus*, 72, 82, 87  
     *breviflorus*, 94

- candidus, 80
- centranthifolius, 214
- cobaea, 79
- cristatus, 80
- glaber, 75
- gloxinioides, 82
- grandiflorus, 79, 94
- heterophyllus, 82
- palmeri, 82
- parishi, 82, 214
- purpureus, 80
- spectabilis, 82
- strictus, 73
- unilateralis, 75, 214
- Penzigia incana, 97
- Petunia hybrida, 82
- Phacelia campanularia, **7**, **16**, 42, 124
  - grandiflora, **31**, 43, 87, 89, 124
  - parryi, **30**, 43
  - tanacetifolia, **29**, 127
  - viscosa, 43
  - whitlavia, **14**, **30**, 43, 125
- Philadelphus coronarius, 72, 91
  - lewisii, 93
- Phleum alpinum, 243
  - pratense, 243
- Phlox divaricata, 93
- Pieris floribunda, 79, 93
- Plantago lanceolata, **76**, **77**, 97, 226
- Poa, 243
  - annua, **Fig. 8**, 72, 272
- Polygonatum commutatum, 80, 94
- Polygonum bistorta, **55**, 173, 196
- Populus, 220
- Potentilla, 196, 215
  - arguta, 80, 94
  - gracilis, 72, 99, 159
  - rubricaulis, 73, 94
- Primula veris, 72
- Prunus, 220
- Psilostrophe cooperi, **37**, 82, 97
- Psoralea floribunda, 80, 94
  - tenuiflora, **73**
- Purshia tridentata, 93
- Quercus agrifolia, 41
- Ranunculaceae, 213
- Ranunculus acris, 72, 75, 94
  - repens, 72
- Raphanus sativus, **34**, 72, 87, 88, 89, 96, 126
- Redfieldia flexuosa, 81
- Robinia, 95
  - hispida, 93
- Rosa acicularis, 191
  - engelmanni, **61**, 191
  - sayi, **61**, 191
- Rosmarinus officinalis, 82
- Rubus strigosus, 159
- Rudbeckia amplexicaulis, **16**, 80, 87, 88, 126
  - bicolor, 32, 96, 112, 113
  - hirta, **46**, **70**, **71**, 72, 82, 159, 172, 202
    - laciniata, 72
- Ruellia ciliosa, 75, 94
- Ruta graveolens, 73, 82
- Salpinglossis sinuata, 73, 82
- Salvia argentea, **22**, 96
  - farinacea, 79, 82
  - grandiflora, 226
  - greggi, 82, 94
- Sanguinaria canadensis, 79, 94
- Saponaria officinalis, 82, 96, 99
- Sarracenia purpurea, 94
- Scabiosa atropurpurea, 73
- Schizachne purpurascens, 75
- scrophularia marilandica, 81
  - nodosa, 75
- Scutellaria galericulata, 80, 94
  - resinosa, **48**, 79, 172
- Sedum, 196
  - roseum, **53**, **65**, 173, 201
- Senecio, 238
  - amplectens, **81**, 238
  - aureus, 238
  - bigelovi, **80**, 238
  - cernuus, **80**, 160, 238
  - croceus, **83**, 201, 238, 241
  - fendleri, **61**, **82**, 159, 160, 191, 238
  - fremonti, **82**, 238
  - salignus, 82
  - taraxacoides, **65**, **81**, **82**, 201, 238
  - vulgaris, 73
- Shepherdia argentea, 93
- Sidalcea neomexicana, 73, 80
- Sieversia, 196
- Silene acaulis, **63**, 199, 211, 213
  - virginica, 94
- Silphium integrifolium, 81
  - laciniatum, 81
  - perfoliatum, 81
  - terebinthinaceum, 81
- Sisyrinchium angustifolium, 87, 94
  - bellum, 97
  - bermudianum, 223
  - striatum, 98
- Smilacina resinosa, 80
  - stellata, **60**, 191
- Solanum douglasii, **5**, **22**, 82, 87
  - nigrum, 73
  - sanitwongsi, 82
  - wallacei, 82
  - xanti, 82
- Solidago, 238
  - arguta, 73, 82
  - canadensis, 73, 82, 94, 95, 99
  - clongata, 238
  - humilis, **71**, **79**, 73, 82, 160, 201, 238
  - h.nana, **8**, 73
  - lateralis, 238



- missouriensis*, **46**, 73, 82, 172, 238  
*multiradiata*, 238  
*nana*, **79**, 94  
*nemoralis*, **62**, 238  
*odora*, 94  
*rigida*, **62**, 73, 81, 82  
*sempervirens*, 81  
*serotina*, 81, 238  
*spathulata*, 238  
*speciosa*, **62**, 81, 238  
*spectabilis*, 238  
*virgaurea*, 73, 82, 238  
*v.nana*, 201  
*v.multiradiata*, 236  
*Sonchus oleraceus*, 73, 82  
*Sphaeralcea ambigua*, 96  
*Sporobolus airoides*, 241  
     *asper*, 99  
     *cryptandrus*, 73, 75  
     *poireti*, 82  
     *wrightii*, 80, 97, 241  
*Statice limonium*, 82  
*Stanleya pinnata*, 79, 83, 96  
*Stellaria alpestris*, 94  
*Stipa*, 132, 243, 247, 258, 260  
     *capillata*, 73, 247, 260  
     *columbiana*, 247  
     *comata*, 73, 247, 260  
     *eminens*, 247  
     *gigantea*, 73, 97, 99  
     *hyalina*, 83, 97, 98, 99  
     *lettermanni*, 247  
     *leucotricha*, 73, 83, 88, 89, 99, 247, 260  
     *minor*, 247  
     *mucronata*, 260  
     *neesiana*, 260  
     *neomexicana*, 75  
     *papposa*, 83, 98  
     *pennata*, 73  
     *pringlei*, 73, 83  
     *pulchra*, 83, 87, 89, 97, 99, 247, 260  
     *p.gracilis*, 97  
     *setigera*, 41  
     *sibirica*, 247  
     *spartea*, 75, 247  
     *speciosa*, 97  
     *tortilis*, 98, 99  
     *vaseyi*, 247  
     *viridula*, **39**, 80, 133, 247  
     *williamsi*, 75  
*Teucrium botrys*, 73  
*Thalictrum alpinum*, **64**, 201  
     *dioecum*, 79, 94  
     *fendleri*, 225  
     *polygamum*, 79, 94  
     *sparsiflorum*, 225  
*Thelesperma filifolium*, 73  
*Tithonia speciosa*, 73  
*Tradescantia virginiana*, 79, 96  
*Tricachne insularis*, 99  
*Trichostema lanatum*, 99  
*Trifolium dasyphyllum*, 202  
     *pratense*, **23**, 73, 99  
*Trillium cernuum*, 79, 94  
     *erectum*, 79, 94  
     *grandiflorum*, 79, 94  
*Triodia albescens*, 75  
     *pilosa*, 75  
*Trisetum montanum*, 241  
     *spicatum*, **64**, 201, 241  
*Triticum aestivum*, 89  
     *sativum*, **9**, **25**, 126  
*Trixis californica*, 82  
*Tropaeolum majus*, 73  
*Tsuga canadensis*, 93  
*Typha angustifolia*, 196  
*Uvularia grandiflora*, 79, 94  
     *perfoliata*, 79, 94  
     *sessilifolia*, 79, 94  
*Vauquelinia californica*, 94  
*Venegasia*, 236  
     *carpesioides*, **78**, 97  
*Verbascum*, 256  
     *blattaria*, 73, 98, 223  
     *phoeniceum*, 73  
     *thapsus*, 73  
*Verbena*, 213  
     *erinoidea*, 83  
     *hastata*, 81  
     *hybrida*, 73  
     *prostrata*, 32, 87, 89, 97, 108, 109, 112, 113, 117  
     *stricta*, 75  
     *urticifolia*, 73, 83, 99  
*Verbenaceae*, 213  
*Verbesina*, 42, 236  
     *encelioides*, **36**, **78**, 73, 83, 87, 96, 98, 99  
*Vernonia baldwini*, 81  
     *noveboracensis*, 81  
*Veronica alpina*, **65**, 201  
     *longifolia*, 73  
     *spicata*, 83, 99  
*Vinca major*, 73  
*Viola canadensis*, 75, 94  
     *cucullata*, 79, 94  
     *nigra*, **28**  
     *pedata*, 79, 94  
     *sagittata*, 79, 94  
     *tricolor*, 87, 88  
*Yucca*, 97  
     *elata*, 97  
     *glauca*, 80, 93  
*Zauschneria californica*, 97  
*Zinnia elegans*, **16**  
*Zygadenus alpinus*, 201  
     *elegans*, 201

## ADDENDA

### Species Specially Mentioned in Graphs and Tables

#### PART I

- Agoseris heterophylla*, 127  
*Agrostemma githago*, 112, 113  
*Antirrhinum hispanicum*, 108, 109, 112, 113, 118  
*Arctotis grandis*, 112, 128  
  
*Baeria gracilis*, 127  
  
*Campanula medium*, 128  
*Chrysanthemum coronarium*, 108, 109, 112, 113, 116, 118  
*Clarkia elegans*, 120  
*Coreopsis l. grandiflora*, 116, 121  
  
*Gaillardia hybrida*, 112  
*Gilia dianthoides*, 127  
     *tricolor*, 127  
*Godetia amoena*, 128  
     *grandiflora*, 121  
  
*Helianthus annuus*, 112, 114, 115  
  
*Madia elegans*, 122  
*Matthiola incana*, 128  
*Mentzelia lindleyi*, 128  
*Mimulus cardinalis*, 108, 109, 112, 113, 114, 116, 123  
  
*Oenothera tricalyx*, 112, 116, 121  
  
*Phacelia campanularia*, 124  
     *grandiflora*, 124  
     *tanacetifolia*, 127  
     *whitlavia*, 125  
  
*Raphanus sativus*, 126  
*Rudbeckia amplexicaulis*, 126  
     *bicolor*, 112, 113  
  
*Triticum sativum*, 126  
  
*Verbena prostrata*, 108, 109, 112, 113, 116

#### PART II

- Achillea m. alpina*, 295  
*Agropyrum scribneri*, 292, 293, 294, 295  
     *violaceum*, 298  
*Allium acuminatum*, 298  
     *cernuum*, 296  
  
*Bromus inermis*, 298  
     *pumpellianus*, 298  
  
*Caltha leptosepala*, 275, 280  
*Carduus eriocephalus*  
     (*Cirsium hookerianum*), 298  
  
*Erigeron glabellus*, 275, 282, 283, 287, 288, 290, 293, 298  
     *macranthus*, 275, 277, 282, 283, 287, 288, 290, 293, 298  
     *subtrinervis*, 292  
     *viscidus*, 293  
  
*Fragaria vesca*, 275, 280, 282, 283, 287, 288, 290  
     *virginiana*, 275, 280, 282, 283, 287, 288, 290  
  
*Geum turbinatum*, 275, 276, 280, 282, 283, 284, 285, 286, 287, 288, 289, 290, 292, 293, 294, 295, 298, 299  
  
*Helianthus annuus*, 274, 275, 276, 277, 278, 279, 281, 283, 284, 286, 288, 290, 297, 298  
*Heracleum lanatum*, 275, 276, 281, 283, 284, 285, 286, 287, 289, 291  
  
*Iris missouriensis*, 292, 293  
  
*Mertensia alpina*, 276, 282, 283, 289, 291, 292, 293, 294  
     *lanceolata*, 275  
     *sibirica*, 275, 276, 277, 280, 281, 283, 284, 285, 286, 287, 288, 289, 290, 292, 293, 294, 299  
     *viridis*, 276, 289, 291, 293  
*Monarda fistulosa*, 292, 299  
  
*Polemonium confertum*, 299  
     *speciosum*, 299  
*Polygonum bistorta*, 292, 294, 295  
*Potentilla gracilis*, 275, 287, 289  
     *hippiana*, 275, 282, 283, 287, 289, 291  
     *nivea*, 276, 277, 282, 283, 287, 289, 291, 299  
     *rubricaulis*, 276, 277, 282, 283, 284, 286, 287, 289, 291, 295

## 332 ADAPTATION AND ORIGIN IN THE PLANT WORLD

- Primula angustifolia*, 276, 282, 283, 287,  
 289, 291  
*Prunus demissa*, 292  
*Rubus strigosus*, 275, 280, 282, 283, 287,  
 288, 290, 292, 293  
*Rudbeckia hirta*, 292, 293  
  
*Sedum roseum*, 299  
*stenopetalum*, 299  
*Senecio aureus croceus*, 277, 281, 283, 284,  
 286, 287, 288, 290, 295  
*bigelovi*, 276, 277, 284,  
 286, 287, 288, 290, 292,  
 293, 295  
*cernuus*, 276, 277, 281, 283,  
 287, 288, 290, 293, 295  
*fendleri*, 275, 287, 288,  
 290, 293  
  
*fremonti*, 292  
*oblanceolatus*, 275, 287,  
 288, 290  
*taraxacoides*, 277, 282, 283,  
 287, 288, 290  
*Smilacina atellata*, 275, 280, 283, 288, 290,  
 292, 293  
*Solidago humilus*, 276, 282, 284, 286,  
 287, 289, 291, 293  
*missouriensis*, 275, 284, 286,  
 287, 289, 291, 293  
*nana*, 282, 283, 284, 285, 286,  
 287, 289, 291, 295, 299  
*nemoralis*, 293, 295, 299  
*speciosa*, 293  
  
*Thalictrum fendleri*, 299  
*Tradescantia virginiana*, 275, 282, 283,  
 289, 291



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